



Temperature variation associated with interannual variability in abundance of juvenile Patagonian toothfish (*Dissostichus eleginoides*) at South Georgia

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Abstract

A detailed understanding of the life cycles of fished species in relation to their environment is important for assessing the impacts of environmental change and informing fisheries management. Here, we examined the abundance of early life stages of Patagonian toothfish (*Dissostichus eleginoides*) in relation to temperature in the waters around South Georgia, located in the rapidly changing southwest Atlantic sector of the Southern Ocean, where a commercial fishery for this species operates. Using scientific demersal trawl survey data spanning almost four decades (1986–2023), we modelled interannual variability in the abundance of juvenile Patagonian toothfish (<26 cm and 26–37 cm size-classes) in relation to temperature conditions during spawning, egg-dispersal, larval-dispersal, and post-settlement development stages. Stage-specific temperatures were derived from depth layers reflecting known vertical distributions of Patagonian toothfish during those stages of development. Long-term trends in temperature were evaluated to identify stages that have potentially experienced the largest changes in thermal conditions over time. Juvenile abundance exhibited marked interannual variability, alongside an apparent long-term decline from 1987 to 2023. Interannual variability was strongly correlated with sub-surface temperatures during spawning and egg dispersal, with cooler temperatures corresponding to lower abundance. While the underlying mechanisms require further investigation, we discuss several hypotheses for these temperature relationships, including the possibility that temperature acts directly or as a proxy for other factors, such as oceanographic processes affecting the transport and retention of early life stages. Our findings provide insight into drivers potentially influencing Patagonian toothfish recruitment and population dynamics, highlighting the importance of considering environmental conditions throughout the water column and across key developmental stages in fisheries management, and identifying priorities for future research.

Keywords Southern Ocean ecosystems, Patagonian toothfish, fisheries management, life history, ocean temperature, climate change

Introduction

Understanding how environmental conditions shape the abundance and dynamics of harvested fish species is fundamental for effective fisheries management. This is important at high latitudes, where marine ecosystems are experiencing rapid physical change and species often exhibit narrow thermal tolerances (Frainer et al. 2017, Campana et al. 2020). Sensitivity to environmental variability differs among life stages, reflecting differences in physiology, dispersal potential, vertical and horizontal habitat use, and trophic ecology (Collins et al. 2005, Freer et al. 2019). This sensitivity can be especially pronounced during early life stages

when environmental conditions can play a critical role in determining survival and recruitment success. Temperature is a key driver, with demonstrated effects on development, growth, survival, and recruitment across a range of high-latitude fish species such as Arctic cod (*Boreogadus saida*) and Walleye pollock (*Theragra chalcogramma*) (Laurel et al. 2018, Huserbråten et al. 2019, Levine et al. 2023).

Despite their importance, species-environment relationships for early life stages remain comparatively understudied for many exploited species and are consequently underrepresented in stock assessment models and fisheries management (Gross and Hoenig 2025). However, life history considerations are critical, with ef-

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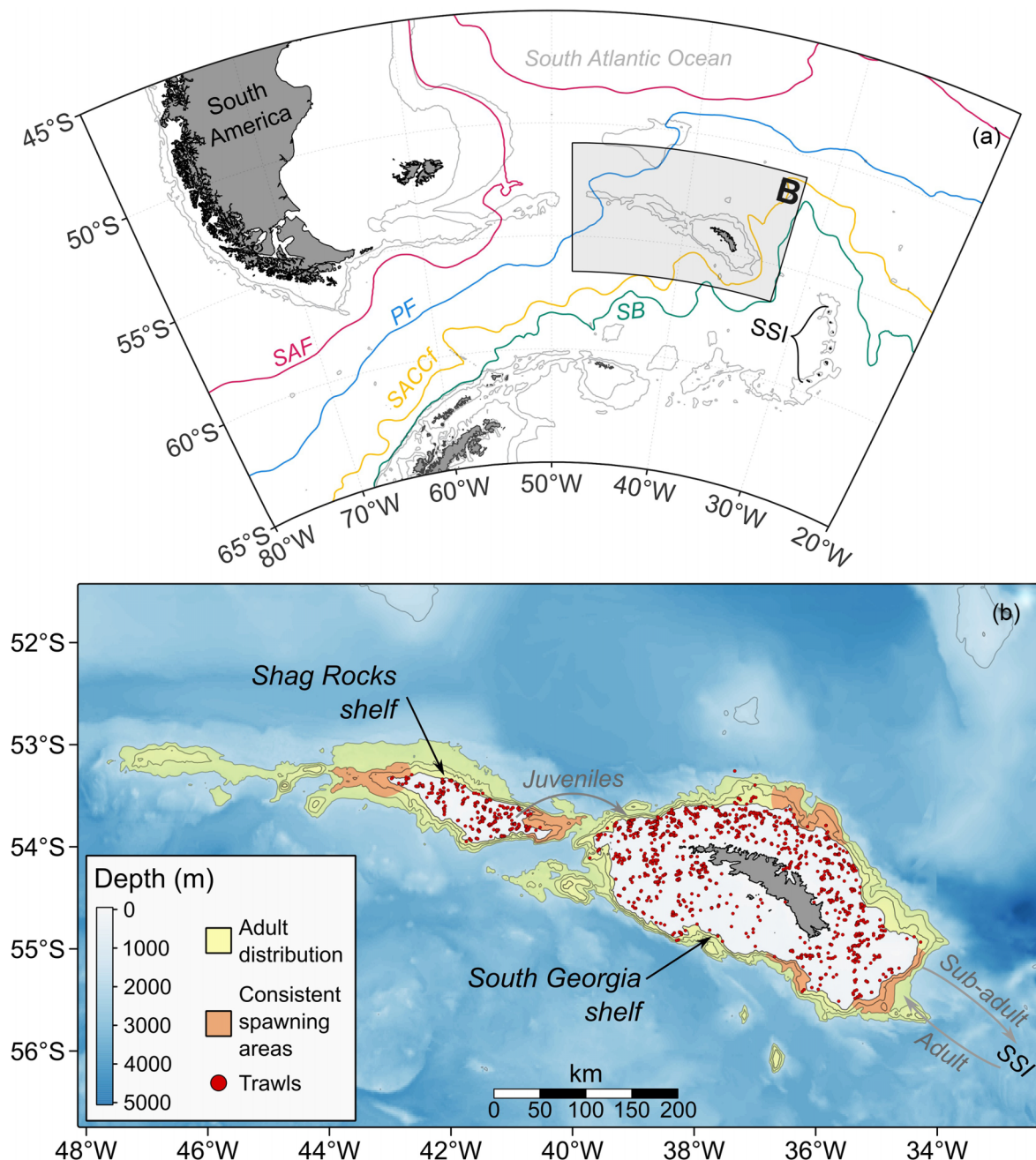


Figure 1 The location of South Georgia and the surrounding shelf area in the southwest Atlantic are shown in relation to South America (a), along with the location of major oceanographic features (SAF = Subantarctic Front, PF = Polar Front, SACCF = Southern Antarctic Circumpolar Current Front, SB = Southern Boundary of the Antarctic Circumpolar Current; taken from Park and Durand 2019) and the South Sandwich Islands (SSI) chain. The South Georgia and Shag Rocks shelf is shown in detail (b), with information on the distribution of adult Patagonian toothfish (*D. eleginoides*) (between 500 and 2000 m isobaths) and known spawning grounds (from Bamford et al. 2024), and locations of demersal trawls used throughout analyses. Bathymetry data were sourced from the ETOPO 2022 dataset (NOAA 2022), and contour lines represent 500, 1000, 1500, and 2000 m isobaths (a: 500 and 2000m only).

fects on early life stages strongly connected to the success or failure of adult populations (Howard et al. 2024). Improving understanding of the effects of environmental conditions during these early phases is essential for anticipating the impacts of climate change and incorporating such knowledge into management decisions.

This study focuses on the Patagonian toothfish (*Dissostichus eleginoides*; Gill and Townsend 1901), a commercially important notothenioid species with a circumpolar distribution around sub-

Antarctic islands and continental shelves. The analysis is centred on the South Atlantic sector of the Southern Ocean, specifically the population in the waters around South Georgia and Shag Rocks (Fig. 1). Together with fish found in the waters around the northern South Sandwich Islands (SSI), at the southern limit of the species' latitudinal range, this population is considered to be a largely discrete stock (Collins et al. 2010, Arkhipkin et al. 2022, Soeffker et al. 2022). South Georgia and Shag Rocks are part of the northern Scotia Arc, with shelves (average depth around 200 m),

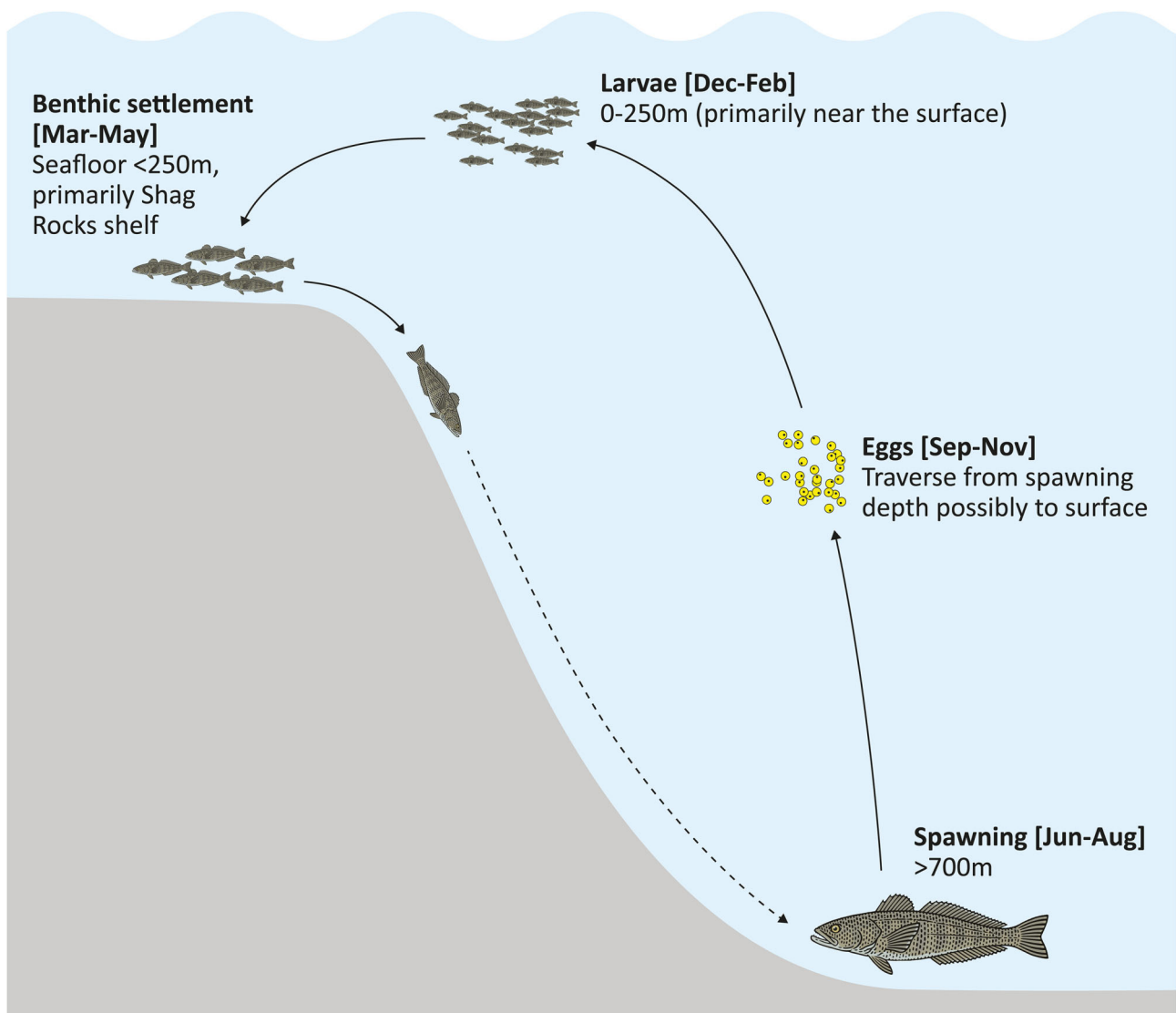


Figure 2: Schematic depicting the four stages of Patagonian toothfish early development with associated depth ranges, noting exact ranges are uncertain: principal spawning (June–August; 700–1000 m and potentially deeper, with known adult distribution extending to ~2000 m), pelagic eggs (September–November; rising from spawning depths potentially to the surface), pelagic larvae (December–February; near-surface), and post-larval benthic settlement (March–May, majority at seafloor depths < 250 m) (see Introduction and Methods for further details).

separated from each other by a 2000 m deep passage, and lie in the path of the Antarctic Circumpolar Current (ACC), which flows north-eastwards across the Scotia Sea. The ACC comprises several deep-reaching fronts associated with water mass distribution and horizontal gradients within the water masses (Orsi et al. 1995). South Georgia and Shag Rocks are situated between the Polar Front, located to their west and north, and the Southern ACC Front (SACCF), which follows the South Georgia shelf in an anti-clockwise direction from the southwest until turning northwards along the northern shelf (Fig. 1). Oceanic conditions at Shag Rocks, located closer to the Polar Front than South Georgia, are generally warmer throughout the water column than at South Georgia, which is more strongly influenced by the SACCF, cooler subpolar waters and glacial run off. Temporal variability in the locations of both fronts (e.g. Boehme et al. 2008, Combes et al. 2023) affects the oceanographic conditions at Shag Rocks and South Georgia, superimposed on longer-term changes in ocean temperature, winds

and circulation patterns (Whitehouse et al. 2008, Cavanagh et al. 2021, Hogg et al. 2021).

The implications of such ongoing environmental change for Patagonian toothfish are not well understood (IPCC 2019, Jones et al. 2026). During its life cycle, the species undergoes pronounced ontogenetic shifts that expose individuals to a range of conditions (Fig. 2). This includes a pelagic stage in which eggs and larvae inhabit surface and near-surface waters, where their development and survival may be influenced by sea surface temperature (SST) (North 2002). Following settlement, juveniles occupy shallow demersal habitats, for this region particularly around Shag Rocks (Fig. 1), which may be associated with comparatively warmer local conditions (Jones et al. 2026). With increasing size and age, individuals progressively move into deeper waters of ~700–1000 m depth (although the known distribution extends to ~2000 m), with adults typically distributed around the continental shelf margin (Collins et al. 2010). Spawning takes place

during the austral autumn and winter, generally along the continental slope of South Georgia and Shag Rocks (Bamford et al. 2024; Fig. 1), the dynamics of which may be influenced by environmental factors, including temperature (Everson and Murray 1999, (Brigden et al. 2017, 2019, Boucher 2018, Bamford et al. 2024).

In this region, Patagonian toothfish underpin a high-value deepwater longline fishery, managed domestically within the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) framework (Agnew 2000, 2004, Collins et al. 2010). Management advice is based on an age-structured stock assessment model (Earl et al. 2024, Earl and Readdy 2024), which integrates groundfish survey abundance and age composition, tag-recapture rates, catch age compositions, catch-per-unit-effort (CPUE), and biological information (Masere et al. 2024). Current management is based on a 35-year projection (Constable et al. 2000), where estimates of historic recruitment are used to determine the magnitude and variability of future recruitment. Under ongoing environmental change, however, these baselines may be less reliable for predicting future population dynamics (Earl et al. 2024, Ouzoulis et al. 2024, Bessell-Browne et al. 2025). In addition, although distribution and biology are monitored for change, environmental parameters are not explicitly incorporated into the assessment framework (Welsford 2023). Work is underway within CCAMLR to refine recruitment assumptions used in projections. Alongside this, Management Strategy Evaluation (MSE) approaches are being developed to evaluate the robustness of harvest strategies under a range of scenarios, including those involving changing environmental conditions.

Building on previous work in this system, showing that depth and temperature strongly structure Patagonian toothfish distribution (Jones et al. 2026), this study focuses specifically on variability in juvenile abundance in relation to temperature conditions during early development stages. By combining long-term scientific groundfish survey data with temperature information, the analysis assesses thermal conditions throughout the water column, corresponding to key developmental stages from spawning through to benthic settlement, in relation to juvenile Patagonian toothfish abundance. This work provides insights into the role of environmental conditions during critical developmental windows, important to population assessments and fisheries management under climate change.

Methods

Demersal trawl survey data

Data on distribution and abundance of Patagonian toothfish were obtained from scientific demersal trawl surveys on the South Georgia and Shag Rocks shelves undertaken approximately every 2 years between 1986 and 2023 (Fig. 1; see Table S1 where S refers to *Supplementary materials*). Sampling methodology has been consistent over time, comprising 30-min demersal trawls (120-foot otter trawl, 18–20 m wingspread, 3–6 m headline height, 40 mm cod end mesh; Belchier 2013) towed at a ship speed of ~3 knots, predominantly carried out during daylight hours (94% between nautical twilight at dawn/dusk, $n = 1776$). Surveys occurred mainly during the austral summer (November–February), with

exceptions in 1997 and 2007 (August–September), 2008 (April), and 2021 (May). Sampling encompassed the continental shelf areas of South Georgia and Shag Rocks at depths from 75 to 917 m, although 95% of trawls were at depths shallower than 330 m. Nearshore and shallower areas (< 100 m), and areas directly south of South Georgia, were sampled less frequently due to limitations in accessibility and seabed suitability (see Hollyman et al. 2021). For each trawl, total Patagonian toothfish abundance was recorded together with trawl depth, distance, and horizontal opening (wingspread). For most trawls (94% of trawls that captured at least one toothfish, $n = 813$), each toothfish was measured (total length to the nearest cm below), enabling catch totals to be separated into size classes. Trawls that captured toothfish but lacked associated size-frequency data ($n = 20$) were excluded from further analysis. In the remaining trawls ($n = 31$), typically those where many toothfish were captured, a representative subsample of individuals was measured (median = 30 fish, range = 2–400), allowing for catch totals for each size-class to be reconstructed based on the proportions of measured individuals.

Size distributions and construction of size-classes

Size frequency data were used to identify size-classes, putatively representative of 1 to 6+ (adult) age groups, based on discrete modes represented in size distributions among years (Table 1) and guided by known growth rates in juvenile Patagonian toothfish (~100–120 mm per year; Collins et al. 2010). The total number of individuals caught in each trawl within each size-class was then enumerated based on measured size and size-class limits to obtain size-class-specific counts for each trawl (Table 1). While size-class limits were generally applicable across most years, they were modified to account for differences in survey timing, most notably for surveys performed in April–May (2008, 2021), September (1997, 2007), or early December (1987, 1988; Table S1), so that single-year cohorts were not divided among size-classes. CPUE (individuals km^{-2}) was also calculated based on individuals caught per area swept (trawl distance $\times$ wingspread; km^2) (Hollyman et al. 2021). For each size-class, the mean CPUE per survey was then calculated, along with its 95% confidence interval via bootstrap resampling ($n = 1000$ permutations). This was calculated separately for the Shag Rocks and South Georgia shelf areas to investigate changes in abundance through time. Given that much of the analysis focuses on the abundance of the two smallest size-classes (< 26 , 26–37 cm), the term juvenile is used to refer to these to distinguish them from the larger size-classes.

Analyses of temporal variation in abundance of early life-stages at Shag Rocks

Interannual variability in abundance was investigated for the two juvenile size-classes in relation to temperature during early development stages. For these analyses, only trawl data from the Shag Rocks shelf were used as these size-classes were rarely caught on the South Georgia shelf (2% and 7% of < 26 and 26–37 cm fish captured; $n = 3737$ and 2839, respectively; see Jones et al. 2026); results are therefore only applicable to variation at Shag Rocks.

Table 1. Size-classes applied to Patagonian toothfish (*D. eleginoides*) caught in groundfish surveys at South Georgia and Shag Rocks. Ages are based on growth rates in Collins et al. (2010) and are indicative only, and larger size-classes may encompass individuals spanning 2 or more years of age.

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

^aThe term juvenile is used when describing analyses or results associated with these two size-classes.

Furthermore, analyses were performed independently for both juvenile size-classes, rather than just for the smallest size-class, because catches of fish measuring < 26 cm have been near-absent in particular years, despite the occurrence of a strong 26–37 cm size-class in the following year. This discrepancy may arise due to gear selectivity, size-dependent net-avoidance behaviour, or because of the more localized and patchy distribution of the smallest size-class (Jones et al. 2026).

To inform these analyses, daily temperature fields for the study region (50–64°S, 30–50°W) were extracted from two different products available through the Copernicus Marine Service. Sea surface temperature (SST) for the period 1993–2023 was obtained from the Global Ocean and Sea Ice Analysis (OSTIA, <https://doi.org/10.48670/moi-00165>; Donlon et al. 2012, Good et al. 2020) dataset, and consisted of daily maps at 0.05° resolution. 3D temperature fields for full ocean depth for 1993–2023 were obtained from the Global Ocean Physics Reanalysis dataset (GLORYS12V1, <https://doi.org/10.48670/moi-00021>; Lellouche et al. 2021). GLORYS12V1 has a horizontal resolution of 0.083° with 50 standard vertical levels ranging from 1 m thick in the upper levels to 450 m thick at 5000 m, with seafloor temperature provided as an additional output. A comparison of GLORYS12V1 temperature with *in-situ* measurements from a summer survey carried out at South Georgia found that temperatures at depths below 50 m were generally within $\pm 0.5^\circ\text{C}$ of the observations (Saunders et al. 2022). To further examine the ability of GLORYS12V1 to reproduce subsurface water properties in the study region, a comparison was undertaken with additional vertical temperature profile data collected around South Georgia (Fig. S1). This indicated generally good agreement in April and July, although the GLORYS12V1 dataset performed less well in September. As such, conclusions based on subsurface temperature relationships are treated with some caution.

Each daily temperature field was cropped to the 1500 m isobath surrounding Shag Rocks and the South Georgia shelf and then divided at 40°W to distinguish conditions at Shag Rocks from those on the South Georgia shelf where juvenile abundance is typically lower. Using these data, annual mean temperature fields were calculated during four stages of toothfish early development by averaging across days specific to the following stages: spawning (June–August; Bamford et al. 2024), pelagic eggs (September–November; North 2002), pelagic larvae (December–February; North 2002, Belchier and Collins 2008), and post-larval benthic settlement (March–May) (Fig. 2). Given differences and uncertainty regarding the depth distribution inhabited during each developmental stage, average temperatures were calculated for

several depth strata (summarized in Table 2), determined by the vertical distribution of: spawning adults (700–1000 m; Collins et al. 2010); eggs, which rise from ~1000 m potentially to the surface, although few eggs have been captured at South Georgia (seven records at depths of 0–500 m; North 2002); pelagic larvae, which have mostly been caught in upper layers of the water column (23 of 43 larvae caught at depths of 0–3 m, 18 of 43 caught at depths of 3–250 m; North 2002); and post-larval fish following settlement to the benthos (majority at seafloor depths < 250 m; groundfish survey dataset). As spawning occurs around South Georgia and Shag Rocks (Bamford et al. 2024), temperature measures for spawning, egg, and larval stages were calculated separately for both South Georgia and Shag Rocks to ascertain which, if any, season by regional division had the strongest correlation with juvenile abundance. However, because only juvenile abundance from Shag Rocks was included, only temperature measures from Shag Rocks were tested for the benthic settlement time-window (March–May). Annual temperature measures for each stage were then assigned to surveys and size-classes based on the presumption that fish measuring < 26 cm present in January (typical survey timing; Table S1) of year Y likely resulted from spawning in June–August of year Y-2, with temperature measures for subsequent developmental stages (egg dispersal, larval dispersal, post-larval settlement) assigned accordingly. These analyses were limited to groundfish surveys from 1997 to 2023 ($n = 19$ surveys), as GLORYS12V1 data used to inform seafloor and midwater temperature covariates were only available from 1993 onwards, which meant that temperature data were only available for surveys after 1995 due to the temporal lags investigated.

Trawl counts for each of the two juvenile size classes (< 26, 26–37 cm) were used as the dependent variable, allowing us to control for differences among trawls (i.e. depth, spatial arrangement) unrelated to interannual variation in abundance. For each size-class, a set of Generalised Additive Mixed Models (GAMM; Wood 2011) were fitted, assuming counts followed a negative binomial distribution (family = nb, log-link). Variations of a null model without temperature effects, but with survey random effects, an offset for log swept-area, and smooths for depth and spatial variation, were initially explored (see *Supplementary materials*). All smooth functions were thin-plate regression splines (basis = 'tp'), apart from spatial effects that were specified by a two-dimensional Gaussian process smooth with different spatial range parameters included to account for spatial autocorrelation among sampling locations (Kammann and Wand 2003, Hefley et al. 2016). Terms included in the 'best' null model, identified based on Akaike's Information Criterion (AIC), were then kept constant across all subsequent mod-

Table 2. Description of temperature covariates and rationale for their use in analyses of interannual variation in abundance of juvenile Patagonian toothfish at Shag Rocks.

Depth strata	Stages	Rationale
Surface: SST	Egg (Sep–Nov) Larvae (Dec–Feb) Settlement (Mar–May)	Temperature potentially experienced by eggs and/or pelagic larvae if within surface mixed layer
Midwater: 110–267 m [23–27]	Spawning (Jun–Aug) Egg (Sep–Nov) Larvae (Dec–Feb)	Temperature potentially experienced by eggs and/or pelagic larvae in water column
Midwater: 267–454 m [28–30]	Spawning (Jun–Aug) Egg (Sep–Nov) Larvae (Dec–Feb)	Temperature potentially experienced by eggs and/or pelagic larvae in the water column
Seafloor: < 267 m	Spawning (Jun–Aug) Settlement (Mar–May)	Temperature potentially experienced by initially benthic eggs and juveniles following benthic settlement
Seafloor: 644–1063 m	Spawning (Jun–Aug)	Temperature potentially experienced by adults and eggs during spawning at depth

For midwater temperatures, exact depth range endpoints were based on depth limits of the 50 vertical levels within the GLORYS12V1 dataset (<https://doi.org/10.48670/moi-00021>). The corresponding GLORYS12V1 vertical depth level numbers are given in [].

els. Temperature covariates were then added to this null model via additional smooth terms, with each candidate covariate (Table 2) tested in separate models. A continuous trend through time was also tested. Alternate models were compared based on AIC and predictive accuracy calculated via leave-one-out cross-validation, holding out entire surveys ($n = 19$), effectively testing the ability of temperature to predict abundance in an unseen year. Predictive accuracy was quantified using a likelihood-based score (Dormann et al. 2018), equal to the log-likelihood of the held-out data given predictions from the model trained on the remaining data. For interpretability, likelihood scores were converted to a measure of relative predictive accuracy, pD , that varied between 0, where the model performs no better than the null model and explains no interannual variation, to 1 where model predictions are as good as possible within the constraints of explaining interannual variability (see *Supplementary materials* for more details). All GAMMs were fitted using the `gam` function in the `mgcv` package in R (Wood 2011).

To visualize relationships between toothfish size-class abundance and temperature, estimated densities (individuals/km²) before accounting for temperature effects were obtained from the null model for each survey by obtaining model predictions inclusive of survey random effects for a set depth of 150 m and at a central point on the Shag Rocks shelf. This step was necessary to account for the inclusion of depth and spatial effects in the model, and to obtain measures of interannual variability once those effects had been accounted for. A visual representation of temperature relationships was then obtained by using the model to predict density across the range of observed temperature values, with depth and spatial location set equal to the same values as used to obtain the null predictions. Survey random effects were not included in the temperature predictions (effectively set to 0) so that the predicted temperature relationship illustrates the overall, or global, effect estimated by the model. Predictions were obtained for the mean density with uncertainty expressed via 95% confidence intervals.

Analyses of long-term temperature trends

To supplement these analyses, long-term trends in surface, sub-surface (depth: 110–267 m) and seafloor temperatures at Shag Rocks (area bounded by the 1500 m isobath) were examined during spawning (June–August), egg (September–November), larval (December–February), and post-larval settlement (March–May) stages. For each temperature metric, calculated as described in the previous section, trends through time were estimated by fitting a linear model with year as the independent variable using Generalized Least Squares (GLS, package `nlme`; Pinheiro and Bates 2025) with a first-order autoregressive correlation structure (AR1) to account for temporal autocorrelation. Results regarding long-term trends are presented via the estimated mean trend coefficient and its 95% confidence interval.

Exploration of water column temperature variability in relation to juvenile abundance

Following the analyses relating interannual variability in juvenile abundance to temperature, differences in temperature throughout the water column were explored during the spawning period (June–August) between years of low juvenile abundance versus moderate-high juvenile abundance. This characterization was based on putative year-class strength indicated by CPUE on the Shag Rocks shelf for the < 26 and 26–37 cm size-classes. For each year of available data ($n = 26$), year-class strength was characterised as either moderate-high or low, classifying low years as those with year-averaged CPUE at Shag Rocks falling within the lower quartile among all available years. This was performed independently for each size-class to enable us to infer conditions for a greater number of years given the typical biennial timing of groundfish surveys.

The putative spawning time-period associated with each year-class (Jun–Aug, assumed to be 1.5 and 2.5 years prior to the survey for < 26 and 26–37 cm fish, respectively) was identified and labelled according to year-class strength (low versus moderate-high). Cases where spawning periods were classified by CPUE for both juvenile size-classes (surveys separated by 1 year; $n = 12$) agreed in 7 of the 12 cases, with the remainder being predominantly those where the < 26 cm classification was ranked as low and the 26–37 cm classification ranked as moderate (Table S5). In those instances, the 26–37 cm classification of year-class strength was used by default, given concerns raised earlier regarding the consistency of sampling for the smallest size-class. In addition, the classifications of year-class strength based on CPUE were compared to those derived from year random effects extracted from a GAMM containing relationships to account for depth and spatial effects fitted to trawl counts of toothfish (family = negative binomial, fitted using gam in the mgcv package in R; Wood 2011). Both approaches produced similar classifications of year-class strength (see *Supplementary materials*).

Water column temperature characteristics during the spawning period (June–August), averaged across years labelled according to year-class strength, were then examined. Daily temperature fields were extracted from GLORYS12V1 and then explored using two different approaches: (i) a north–south transect across the Shag Rocks shelf (52.5–54°S, 41.5°W), examining how temperature varies with respect to depth-layer (0–650 m) and along the transect; (ii) horizontal maps of temperature at 110–131 m depth for the South Georgia and Shag Rocks region. This latter dataset corresponds to temperature at or below the mixed layer (typically 100–150 m during June–August in the vicinity of South Georgia; Dong et al. 2008). In each case, the extracted data (daily; June–August) were averaged over time as classified based on year-class strength to ascertain average water column conditions associated with low juvenile abundance versus moderate-high abundance.

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

Results

Size distributions and interannual variability

Size distributions of Patagonian toothfish captured in ground-fish surveys were indicative of sporadic pulses of juvenile fish at Shag Rocks, with cohorts of < 26 cm toothfish present in seven of the ten surveys from 1987 to 2003, followed by an absence until 2019 (Fig. 3). However, 26–37 cm toothfish were present in years between 2004 and 2019 (i.e. 2006, 2010, 2012; Fig. 3), suggesting that the smallest size-class may not be reliably sampled. Strong cohorts were frequently present in sequential survey years, with particularly dominant cohorts first detected in 1990, 2003, 2010, and 2019 accounting for the majority of fish captured on the Shag Rocks shelf over the following 2–5 years (Fig. 3). However, while year-classes were often initially distinct, widening size distributions and overlapping size among year groups prevented identification of individual cohorts for fish larger than ~55–60 cm. In comparison to Shag Rocks, juvenile fish (< 26 cm, 26–37 cm) were rarely captured on the South Georgia shelf,

with CPUE of each size-class frequently more than 1–2 orders of magnitude higher on the Shag Rocks shelf compared to the South Georgia shelf (Fig. 3). Size distributions on the South Georgia shelf were dominated by larger-sized individuals (median = 53 cm, compared to 42 cm on the Shag Rocks shelf), and lacked the visible cohorts present on the Shag Rocks shelf (Fig. 3). The difference in CPUE between Shag Rocks and South Georgia decreased with each increase in size-class, with CPUE being almost equivalent between the two shelf locations for the largest size class (> 66 cm), consistent with a pattern of dispersal toward the South Georgia shelf from initial settlement grounds at Shag Rocks (Fig. 3).

Survey-averaged CPUE of the < 26 cm size-class on the Shag Rocks shelf varied by more than three orders of magnitude among years, varying from an unusually high value of 9000 individuals km^{-2} in 1990 to zero in multiple years between 2004 and 2017 (Fig. 3). While CPUE for this size-class appears to have increased in recent years (1999–2023), values remain lower than those typically observed prior to 2000 (Fig. 3). Broadly similar patterns were observed on the South Georgia shelf (Fig. 3). Average CPUE of the 26–37 cm size-class at Shag Rocks varied less among surveys, and prior to 2006 exceeded 100 individuals km^{-2} in the majority (8 of 12) of years (Fig. 3). From 2006 onwards, CPUE alternated between periods of low CPUE (2007–2009, 2013–2021) followed by periods of CPUE similar to those recorded prior to 2006 (2010–2012, 2023; Fig. 3). The 2023 survey recorded the highest CPUE of 26–37 cm fish in more than a decade across both shelf locations (Fig. 3).

For larger size classes (48–57, 58–66, > 66 cm) CPUE has been broadly consistent through time at Shag Rocks (Fig. 3). However, CPUE of the 48–57 and 58–66 cm size-classes at South Georgia decreased from 2009 onwards (mean CPUE 2009–2019 = 1.7 and 1.9 individuals km^{-2} for 48–57 and 58–66 cm size-classes, respectively) compared to the previous 10 years (mean CPUE 1998–2008 = 7.3 and 7.1 individuals km^{-2}), which matches the generally lower CPUE of the 26–37 cm size-class from 2007 until 2019 (Fig. 3). However, lower interannual variability of CPUE for the larger size-classes suggest that relative abundance of adults may be buffered from the variability in juvenile abundance.

Abundance of early life-stages in relation to temperature variability

Size: <26 cm

Models fitted to counts of <26 cm toothfish on the Shag Rocks shelf indicate a positive correlation with temperature during egg and larval dispersal phases, irrespective of the depth at which temperature was assessed (surface or midwater), but no relationship with temperatures during spawning (Fig. 4). The temperature covariate with the highest predictive accuracy was that calculated in midwater over the Shag Rocks shelf during egg dispersal (predictive accuracy score, $pD = 0.69$, indicative of 69% of interannual variability explained by temperature; Table 3) and was suggestive of a 10-fold increase in abundance with temperature increasing from 1.4°C to 1.8°C (Fig. 4). Surface temperatures during the larval-dispersal period and seafloor temperatures during the benthic settlement stage were also positively correlated with abundance but had lower predictive accuracy (Table 3). Inclusion of a continuous

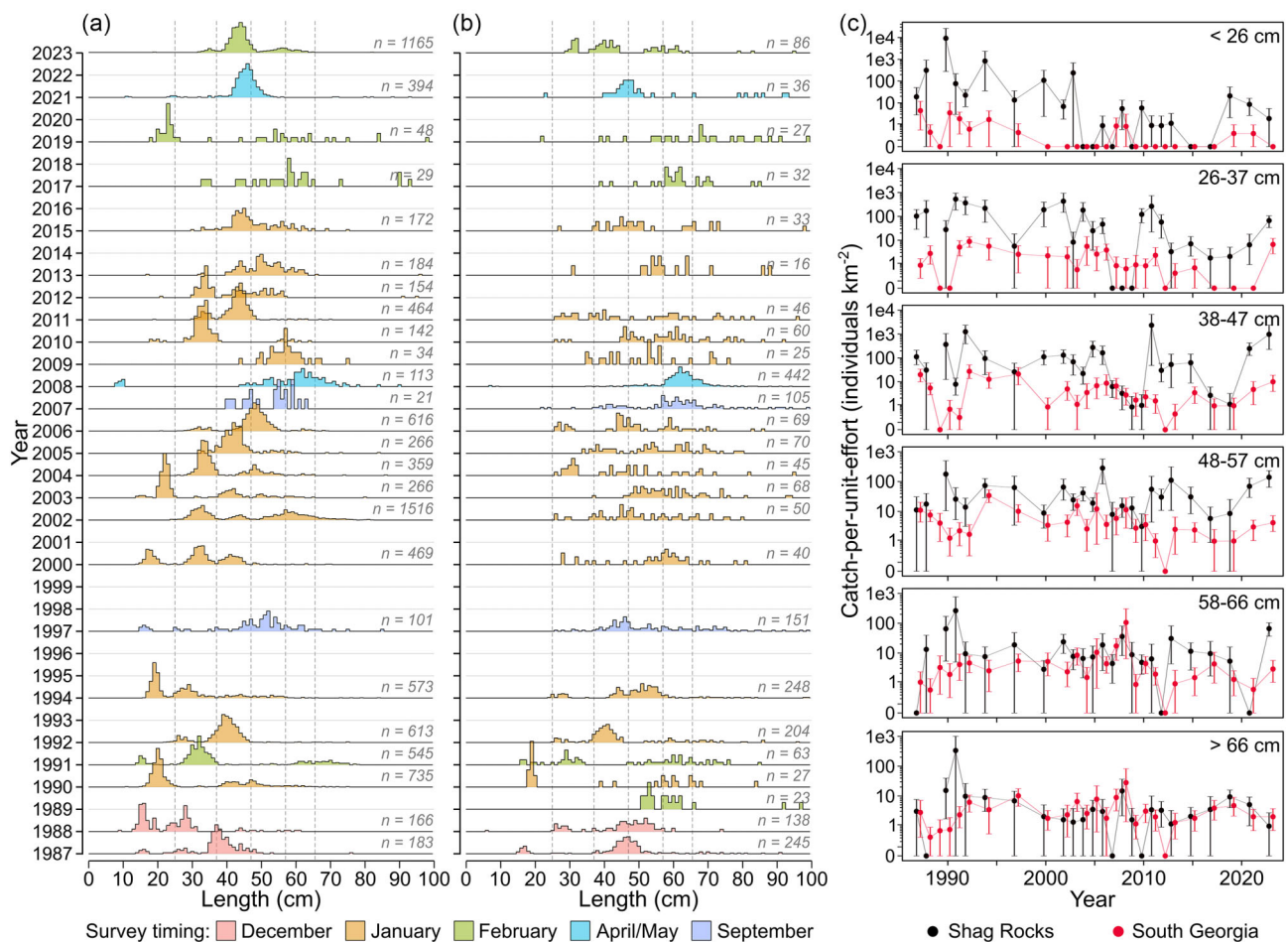


Figure 3 Size distributions of Patagonian toothfish (*D. eleginoides*) caught on the Shag Rocks (a) and South Georgia (b) shelves during groundfish surveys from 1987 to 2023, along with survey-averaged CPUE (individuals per km²) for different size-classes (c; < 26, 26–37, 38–47, 48–57, 58–66, > 66 cm) based on total length. Note that histogram heights in panels (a) and (b) are scaled according to the total number caught within each survey, provided in grey text to the right of each panel, and therefore represent relative, rather than absolute, abundance in a particular survey. Histograms are colour-coded according to the month in which the majority of trawls were performed in a given survey. Size-class thresholds are indicated by dashed vertical lines in panels (a) and (b). Values in panel (c) correspond to the survey-mean CPUE calculated according to counts of individuals caught within each size-class divided by trawl swept area (km²). Error bars indicate the bootstrapped 95% confidence interval of the mean.

trend through time did not change the fitted temperature effects, but when included by itself indicated a decline in abundance from 1997 to 2010, followed by an increase from 2015 to 2023 (Fig. S2). Fitted spatial effects also indicate a highly constrained distribution on the Shag Rocks shelf, largely associated with depth (depth < 200 m; Fig. S3 and S4).

Size: 26–37 cm

Similar to results found for < 26 cm sized fish, models fitted to counts of the 26–37 cm size-class on the Shag Rocks shelf were indicative of a positive correlation with temperature during the egg dispersal stage (Fig. 4d). However, the strongest relationship for this size-class came from models containing temperatures calculated during the spawning time-window (June–August) over the Shag Rocks shelf either at the seafloor (seafloor depth < 267 m, $pD = 0.69$) or in the midwater column at 110–267 m depths ($pD = 0.45$; Table 3). The fitted relationship between abundance and temperature during spawning indicated a peak in abundance at temperatures of 1.65°C (seafloor temperature; Fig. 4c) or 1.9°C

(midwater temperature; Fig. S5), with lower abundance at both higher and lower temperatures. Models containing temperature covariates assessed during larval-dispersal or settlement stages performed worse than the null model, indicating weak to no effect.

Although including a continuous trend through time indicated an overall declining trend in abundance of 26–37 cm toothfish (Fig. S5), models containing this term had lower predictive accuracy both when included alone ($pD = -0.02$; Table S4) and when included with temperature covariates (reduction in pD relative to equivalent models of 0.04–0.13; Table 3). This suggests that long-term patterns may be more strongly characterised by fluctuations in abundance among years, or groups of years, rather than by a continuous trend through time. Fitted spatial effects for the 26–37 cm size-class indicated a deeper and more widespread distribution across the Shag Rocks shelf compared to that found for the < 26 cm size-class (Fig. S6 and S7), consistent with a distributional difference across size classes, with larger individuals occurring in deeper areas.

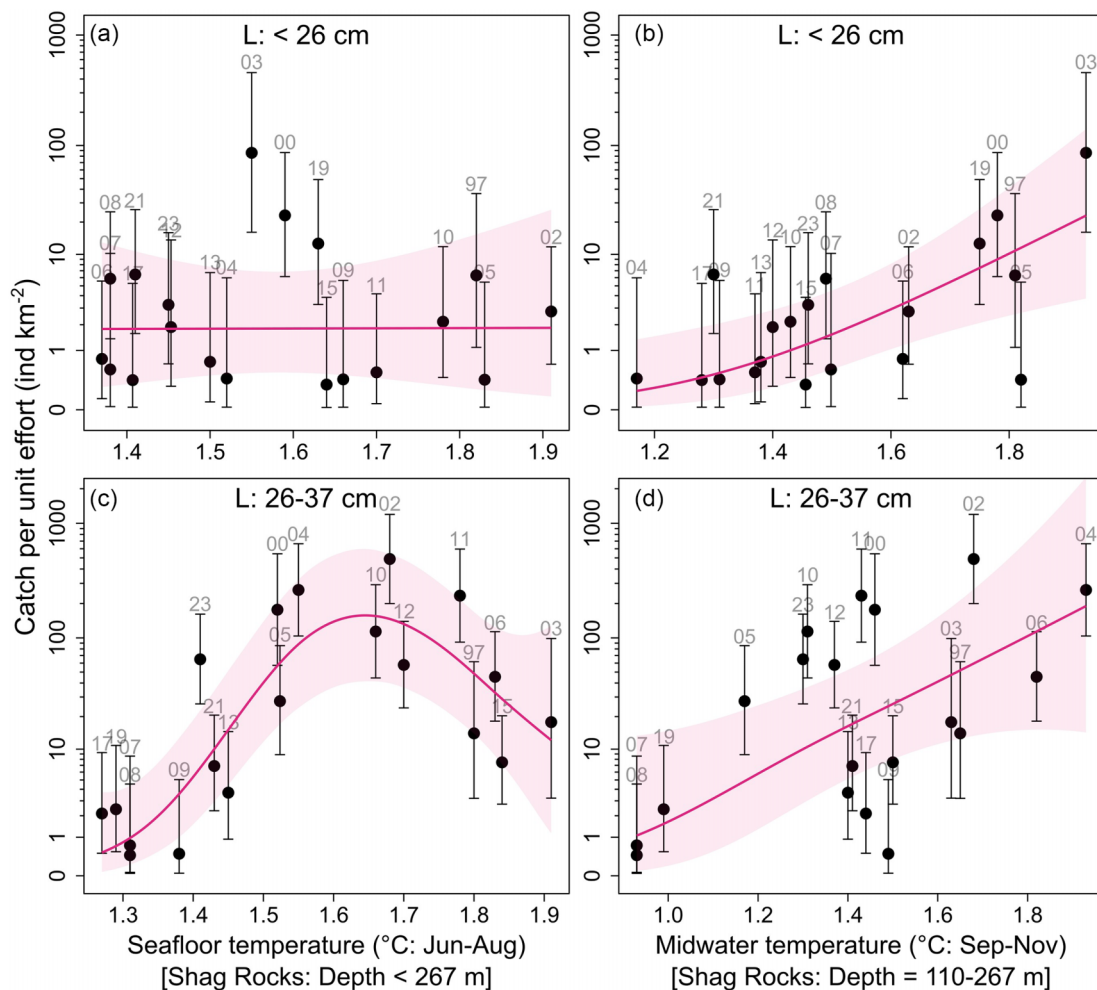


Figure 4 Fitted relationships between observed CPUE (individuals km^{-2}) of juvenile Patagonian toothfish (*D. eleginoides*) on the Shag Rocks shelf and temperature during different stages of early development. Panels correspond to relationships for < 26 cm (a and b) and 26–37 cm (c and d) size-classes for the two temperature covariates that were the best predictors of annual abundance: seafloor temperature on the Shag Rocks shelf calculated during spawning (June–August, a and c), and midwater temperature at 110–267 m calculated during egg-dispersal (September–November, b and d). Points and error bars are the mean ($\pm$ 95% confidence interval) predicted density for a given survey from the null model (i.e. without temperature effects, but including temporal differences via survey random effects), which account for differences in depth and location effects among surveys for each size-class. Lines and shading indicate the predicted relationship and 95% CI from the model fitted with the corresponding temperature effect. Predictions from the null (points and error bars) and temperature-informed models were all obtained for a depth of 150 m and for the central point on the Shag Rocks shelf, and survey random effects were excluded from predictions of the temperature relationship (effectively set to 0) to show the overall, or global, effect.

Long-term trends in temperature specific to stages of early development

Given the importance of temperatures on the Shag Rocks shelf at various stages throughout the early development of Patagonian toothfish, long-term trends in seafloor, midwater (or subsurface; 110–267 m depth), and sea surface temperature were examined during each of the putative spawning, egg, larval, and post-larval benthic settlement stages (Fig. 5). Over a 30-year period, temperature patterns during spawning (June–August) and egg (September–November) stages were characterized by warming in surface layers, alongside an apparent cooling in subsurface and seafloor temperatures (Fig. 5). Surface warming was most pronounced during the egg dispersal time-window, with an average increase of 0.23°C per decade, while subsurface cooling

was most evident during spawning ($-0.1^{\circ}\text{C}/\text{decade}$; Fig. 5). That said, sub-surface temperatures over the most recent 20 years in this dataset (i.e. 2004–2023) have either remained near constant (June–August; trend = 0.03 [95%CI = -0.20 – 0.26] $^{\circ}\text{C}$ per decade for the midwater column temperatures) or have increased (September–November; trend = 0.15 [95%CI = 0.00 – 0.31] $^{\circ}\text{C}$ per decade), suggestive of non-linear changes through time. Temperature patterns during the larval (December–February) and benthic settlement (March–May) stages indicated little overall trend over the same period across depth levels, with the exception of surface temperatures during December–February, which showed an increasing trend of 0.11°C per decade, albeit alongside high interannual variability (Fig. 5). Collectively, these season-specific patterns indicate that temperature conditions have changed the most during periods coinciding with the timing of spawning and egg-dispersal stages of Patagonian toothfish at South

Table 3. Summary statistics for models fitting abundance of <26 and 26–37 cm Patagonian toothfish on the Shag Rocks shelf to temperature conditions during different early development stages (Spawn = Jun–Aug, Egg = Sep–Nov, Larvae = Dec–Feb, Settlement = Mar–May), locations (SR = Shag Rocks, SG = South Georgia), and depth strata.

Stage	Area	Depth	Date	edf	AIC	D ²	pD
<i>Length: < 26 cm</i>							
NULL				21.9	316.8	79.8	0.00
Egg (Sep–Nov)	SR ^a	Midwater (110–267 m)		20.0	315.8	79.1	0.69
Larvae (Dec–Feb)	SR ^a	Midwater (110–267 m)		20.5	318.9	78.4	0.65
Larvae (Dec–Feb)	SG ^b	Surface		22.6	317.6	79.9	0.27
Settlement (Mar–May)	SR	Seafloor (< 267 m)		22.4	319.2	79.4	0.37
NULL			Y	21.5	316.6	79.6	0.24
Spawn (Jun–Aug)	SG	Seafloor (< 267 m)	Y	21.7	316.8	79.7	0.28
Egg (Sep–Nov)	SR	Midwater (110–267 m)	Y	20.9	317.5	79.1	0.63
Larvae (Dec–Feb)	SR ^a	Surface	Y	21.9	317.8	79.5	0.48
Larvae (Dec–Feb)	SG ^b	Midwater (110–267 m)	Y	20.3	316.7	78.9	0.64
<i>Length: 26–37 cm</i>							
NULL				23.1	1029.7	58.9	0.00
Spawn (Jun–Aug)	SR ^a	Midwater (110–267 m)		22.5	1028.3	59.0	0.45
Spawn (Jun–Aug)	SR	Seafloor (< 267 m)		21.8	1027.8	58.8	0.69
Egg (Sep–Nov)	SG ^b	Midwater (110–267 m)		22.8	1028.8	59.0	0.21
Larvae (Dec–Feb)	SG	Midwater (110–267 m)		23.1	1029.6	59.0	0.16
NULL			Y	23.3	1030.2	58.9	–0.02
Spawn (Jun–Aug)	SR	Midwater (110–267 m)	Y	22.5	1028.1	59.0	0.32
Spawn (Jun–Aug)	SR	Seafloor (< 267 m)	Y	22.1	1028.0	58.9	0.65
Spawn (Jun–Aug)	SG ^b	Seafloor (644–1063 m)	Y	23.2	1029.7	59.0	0.13
Egg (Sep–Nov)	SR	Midwater (110–267 m)	Y	22.8	1028.5	59.0	0.09

Statistics shown are the model-estimated degrees of freedom (edf), Akaike's Information Criterion (AIC), deviance explained (D²), and predictive deviance score (pD) calculated via cross-validation. The Date column indicates whether models also included a continuous trend through time. Only those models that improved on the null model (based on predictive scores) are presented; see Table S3–S4 for all model statistics.

^a Temperatures at South Georgia for this season and depth also performed better than the null, but had higher predictive likelihood scores and displayed similar fitted temperature effects.

^b Temperatures at Shag Rocks for this season and depth also performed better than the null, but had higher predictive likelihood scores and displayed similar fitted temperature effects.

Georgia, while remaining relatively stable during later developmental stages.

Exploration of water column temperature variability in relation to juvenile abundance

Prior to years with low juvenile abundance (CPUE of the < 26 cm or 26–37 cm size-class at or below the lower quartile across available years), average temperatures during spawning were characterized by a deeper transition from cold surface waters (< 1.4°C) to warmer subsurface waters (typically > 2°C) when compared to years in which juvenile abundance was high (Fig. 6). In years preceding high juvenile abundance, warmer water conditions (> 1.5°C) prevailed on and above the seafloor at the Shag Rocks shelf, while the same locations were 0.3°C–0.4°C colder in years of low juvenile abundance (Fig. 6). Temperatures at depths 110–131 m were uniformly colder in poor spawning years relative to normal throughout the South Georgia region. Furthermore, warmer water at depths of 100–200 m, which typically covers the Shag Rocks shelf in years of good recruitment, was not present in poor years, with warmer subsurface conditions instead located westward of the Shag Rocks shelf (Fig. 6).

Discussion

Size distributions and interannual variability

The findings reinforce the importance of the Shag Rocks shelf to early life stages of Patagonian toothfish (Collins et al. 2007, Belchier and Collins 2008). Analyses revealed strong interannual variability in juvenile abundance, including multi-year periods of alternating high and low abundance, alongside an apparent slight long-term decline. In contrast, comparable interannual variability was not evident in the larger size-classes (> 48 cm), suggesting that populations of larger (older) fish remaining on the South Georgia or Shag Rocks shelf may be buffered, to some extent, against large year-to-year changes in juvenile abundance. This buffering may reflect limited on-shelf resources constraining the abundance of larger fish and supporting a relatively constant population size. Several mechanisms could potentially contribute to this buffering, including density-dependent mortality, off-shelf dispersal (Collins et al. 2010), and immigration of fish from off-shelf areas. These processes were not directly examined in the present study and should therefore be regarded as hypotheses requiring further investigation. Furthermore, the results indicate that years of strong recruitment are associated with cohorts

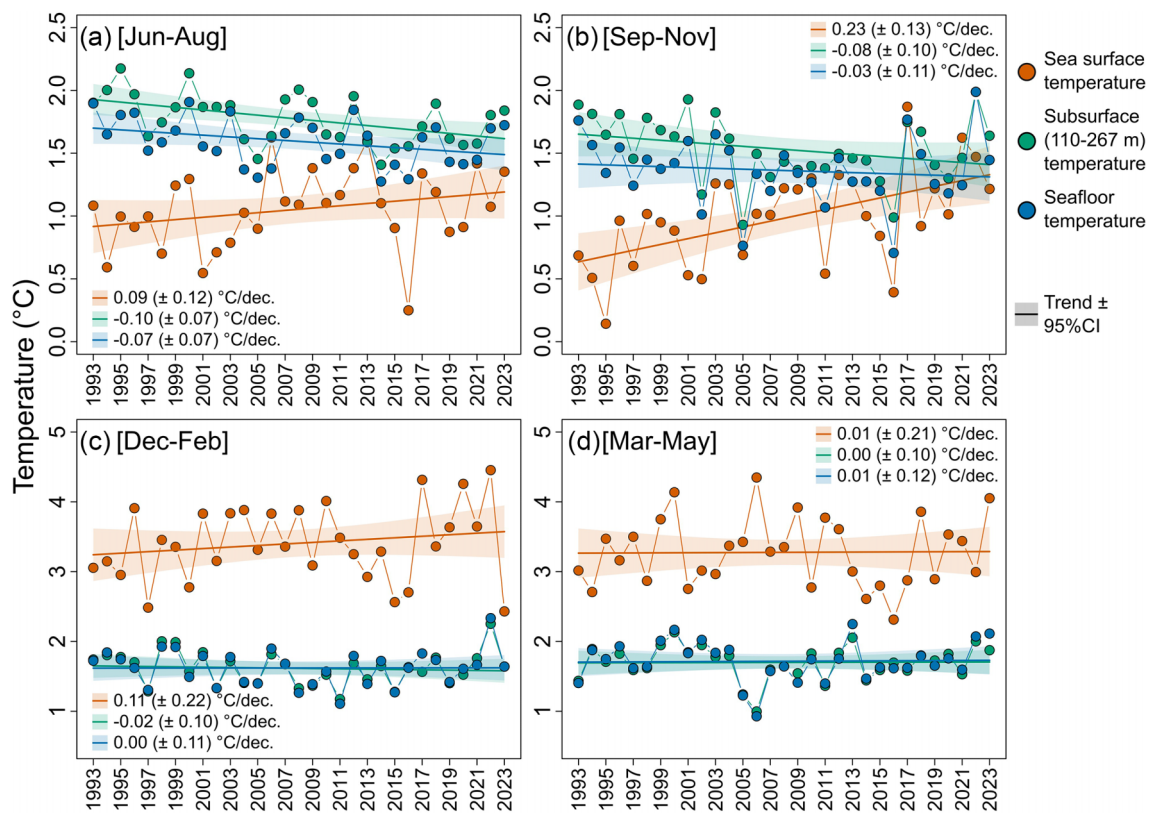


Figure 5 Long-term trends in temperature over the Shag Rocks shelf by time-period and water column strata (sea surface, subsurface, seafloor) specific to early development of Patagonian toothfish (*D. eleginoides*). Panels correspond to seasonal average temperatures calculated per year for June–August (a), September–November (b), December–February (c), and March–May (d), putatively representative of spawning, egg, larval, and post-larval stages of toothfish in the South Georgia and Shag Rocks region, respectively. Subsurface (depth = 110–267 m) and seafloor (depth < 267 m) temperature data were extracted from the Global Ocean Physics Reanalysis dataset, whereas sea surface temperature was obtained from the Global Ocean OSTIA dataset, both archived on the Copernicus Marine Data Store. Trend lines are those from a linear model fitted to the corresponding data, with shading to indicate the 95% confidence interval. Trend estimates and 95% CI are also given in °C/decade.

that tend to persist, dominating size distributions for at least the first 3 years following benthic settlement. The persistence of these strong cohorts may reduce the impact of poorer recruitment in intervening years on overall population size. However, consecutive years of weak recruitment may eventually exceed this buffering capacity, potentially resulting in a decline in overall population size.

Abundance of early life-stages in relation to temperature variability

Positive relationships were found between juvenile Patagonian toothfish abundance and temperature, consistent with the species' broader distribution (Collins et al. 2010). The strongest temperature-abundance relationships occurred within the water column, below the surface mixed layer, for both the <26 and 26–37 cm size-classes (approximately age 1+ and age 2+ toothfish). These were most pronounced at time lags corresponding to early developmental stages, particularly spawning and egg dispersal, which also coincide with periods that have experienced the greatest temperature changes over the past 30 years.

However, temperature relationships differed between the size-classes. Abundances of the smallest size-class displayed a simple positive relationship with temperature during egg dispersal,

whereas 26–37 cm fish exhibited a more complex, domed relationship, with highest abundances coinciding with seafloor and mid-water temperatures of 1.6°C–1.9°C during spawning. In addition, the strongest relationship overall—across size-classes and temperature covariates—was for abundances of 26–37 cm fish in relation to temperatures during spawning, despite the longer time-lag (2.5 years) compared with that evaluated for the < 26 cm size-class. A potential explanation for this discrepancy is that CPUE may be less reliable for the smallest size-class, particularly with respect to gear selectivity and their patchier distribution, which may obscure relationships with environmental variability.

The strong relationship between CPUE of the 26–37 cm size-class on the Shag Rocks shelf and seafloor and subsurface temperatures during spawning gives rise to several connected hypotheses. Whether temperature acts as a direct driver of recruitment success or serves as a proxy for other environmental processes is uncertain. One possibility is that subsurface temperature influences prey conditions around Shag Rocks for larval or post-larval fish, thereby regulating their abundance via prey limitation under certain temperature regimes. Examination of CPUE of 26–37 cm and 38–47 cm size-classes of toothfish in relation to the abundance of yellowfin notothen (*Patagonotothen guntheri*), a primary prey species for juvenile Patagonian toothfish on the Shag Rocks shelf that is also recorded during groundfish surveys (Collins et al. 2008), suggests only a weak positive correla-

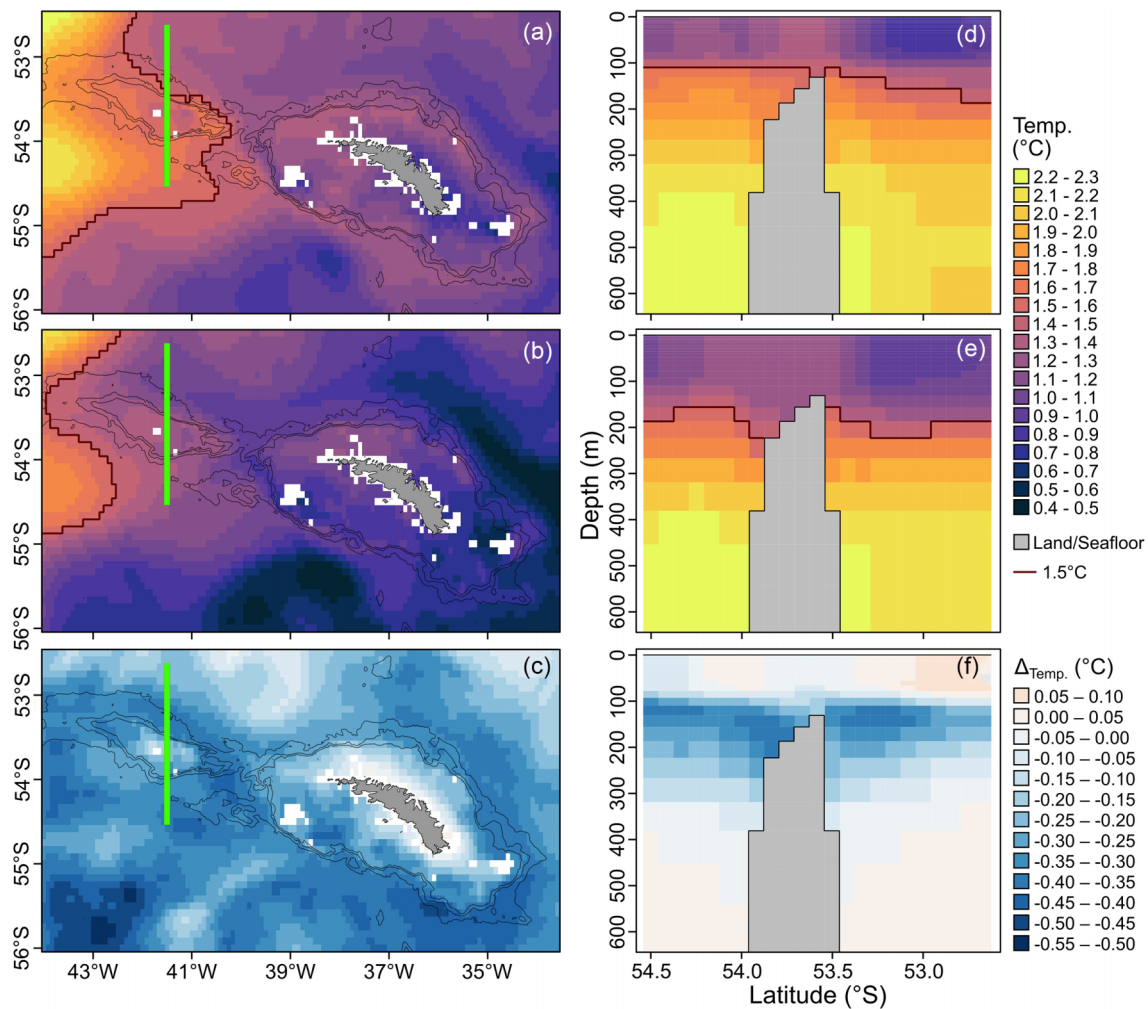


Figure 6 Temperature at depth averaged across years during the Patagonian toothfish (*D. eleginoides*) spawning season (June–August). Panels correspond to the average water temperature at 110–131 m throughout the South Georgia region (a and b), and for a cross-section (vertical rectangle in panels a and b) spanning the Shag Rocks shelf (d and e) showing temperature variation according to depth and latitude. Alternate maps and cross-sections correspond to temperatures averaged over years in which juvenile toothfish abundance was moderate to high (a and d; years = 1995–2003, 2007–2009, 2011, 2017, 2019–2021) versus low (b and e; years = 2004–2006, 2010, 2012–2016, 2018) based on CPUE on the Shag Rocks shelf during groundfish surveys. The difference in temperature maps (c) and cross-sections (f) between the two year-sets is also shown (low abundance minus moderate to high). The 1.5°C isotherm is plotted in (a), (b), (d) and (e) (heavy line). 500, 1000 and 1500 m isobaths are plotted in (a) – (c) (thin lines).

tion with the larger 38–47 cm size-class (Fig. S8), and no correlation with abundance of the 26–37 cm size-class. However, reduced abundance of yellowfin notothen from 2007 to 2009 coincided with a shift from years of moderate abundance of both 26–37 cm and 38–47 cm toothfish to multiple years (2008–2010) of reduced abundance, which may indicate a common or related underlying mechanism. Notably, this period was also accompanied by a shift in seafloor temperatures towards colder conditions on the Shag Rocks shelf that began in 2005 (Fig. 5). Colder conditions may have direct effects on both species, given the observation that yellowfin notothen are restricted to the Shag Rocks shelf, potentially due to intolerance of the lower temperatures on the South Georgia shelf (Collins et al. 2007, 2008), or indirectly through changes in prey community composition important to both yellowfin notothen and juvenile Patagonian toothfish. Further work is required to improve understanding of potential changes in the prey field and corresponding toothfish responses (Ward et al. 2025).

A second hypothesis is that temperature directly influences egg survival and development in Patagonian toothfish, as observed in other species (e.g. Tsoukali et al. 2016, Howard et al. 2024), with cooler subsurface conditions during the spawning season potentially resulting in higher egg mortality or delayed development. The indication of a deeper thermocline and cooler subsurface conditions during the spawning season prior to low recruitment years suggests that eggs traversing the water column in those years may experience more extreme temperature changes at greater depths (Fig. 6). In addition, eggs may occupy cooler water for a period, which could delay or inhibit development. However, this interpretation is predicated on eggs remaining at depths below the mixed layer (100–300 m) for a duration sufficient to affect development. The depth distribution of Patagonian toothfish eggs at South Georgia is poorly understood, and few studies have captured eggs or larvae despite pelagic sampling (North 2002), suggesting that they are either patchily distributed, exhibit net avoidance (larvae), or are present deeper than is typically sampled by

pelagic trawls. Evseenko et al. (1995) reported captures of seven eggs in September–October in the upper 500 m of the water column to the north of South Georgia, suggestive of a pelagic distribution. However, North (2002) and Zhivov and Krivoruchko (1990) have suggested that eggs are initially demersal, with the former based on the absence of eggs in pelagic sampling despite high egg abundance inferred from calculations of population fecundity. More recently, Harte (2021) reported a reduction in egg buoyancy after fertilisation followed by an increase during development, consistent with the possibility of an initial demersal phase followed by a pelagic phase, while egg morphology described by Mujica et al. (2016) appears more consistent with a pelagic distribution. Similar evidence has been reported for the Antarctic toothfish (*D. mawsoni*), whose eggs exhibit positive buoyancy in early development (Ghigliotti et al. 2018, Parker et al. 2021). Taken together, these studies highlight continued uncertainty regarding the vertical distribution of Patagonian toothfish eggs. Nevertheless, an initial demersal phase, coupled with changes in buoyancy during development, would be consistent with the findings in this study, which highlight associations between seafloor and subsurface temperatures during spawning and egg dispersal stages to subsequent juvenile abundance. Improved data on egg depth distribution is essential, as vertical position in the water column strongly influences exposure to temperature, currents, and other environmental drivers. Alternatively, the temperature relationship may reflect broader oceanographic conditions associated with temperature variability, including circulation processes that influence the dispersal and retention of early life stages.

Although the underlying mechanisms require further investigation, temperature at Shag Rocks appears to be strongly associated with juvenile Patagonian toothfish recruitment, with warmer temperatures below the mixed layer during spawning showing the strongest correlation with juvenile abundance in subsequent years. This suggests lower juvenile abundance following spawning periods characterized by cooler temperatures below the mixed layer. Notably, while SST at Shag Rocks has increased at a rate of 0.09°C per decade in recent years, sub-surface temperatures—including seafloor temperatures during the spawning period, which correspond to the depth and timing most indicative of recruitment—do not appear to have increased to the same degree, having decreased at a rate of 0.1°C per decade from 1993 to 2023 and stayed largely static over the last 20 years (2004–2023 trend = +0.03°C per decade; Fig. 5). The lack of warming and presence of multi-year periods of cooler conditions in subsurface layers during the spawning period over the last 20 years (Fig. 5a) may help to explain the apparent decline in juvenile abundance. However, while SST trends are derived from a satellite product and are comparable with rates calculated from *in situ* data by Whitehouse et al. (2008), much of the analyses in this study utilize subsurface temperatures obtained from a global ocean reanalysis dataset (GLORYS12V1). Although multiple observational datasets are assimilated in the reanalysis, the representation of properties including temperature is influenced by the availability of the assimilated *in situ* data (Lellouche et al. 2021), which may affect the trends reported here. Notwithstanding these limitations, the temperature patterns across depth layers point to more complex dynamics than indicated by surface trends alone, highlighting the need for further work to resolve how such variability may influence early development.

Implications for fisheries management

Given the complex life history of Patagonian toothfish (Fig. 2), their important role in the South Georgia ecosystem and the rapid environmental changes in the region, ensuring sustainable fisheries management in the face of future change is essential (Jones et al. 2026). The findings of this study emphasise the importance of considering subsurface thermal structure as well as surface temperature changes when evaluating the effects of climate change (Azarian et al. 2022, Ward et al. 2025). The same considerations would apply to other deepwater species, particularly those whose eggs and larvae traverse the water column. Changing vertical temperature profiles may expose eggs and larvae to conditions that exceed their physiological tolerances. Steep or irregular thermal gradients, such as the transitions described in this study from warmer sea floor temperatures through cooler midwater to warmer surface temperatures, may be particularly consequential. Vertical position and exposure duration likely influence egg and larval development, survival, and timing of settlement, with potential effects carried forward throughout the life cycle.

A further consideration is that model simulations of transport and retention of early life stages of Patagonian toothfish suggest that variability in local ocean circulation affects their retention around South Georgia and Shag Rocks (Brigden 2019). Modelling experiments that combine temperature effects with egg and larval dispersal simulations, including particle tracking, transport modelling, and egg buoyancy, together with *in situ* observations and *ex situ* studies of physiological responses during early development, could provide a more mechanistic understanding of how environmental variability affects recruitment.

Consideration of environmental conditions across key developmental windows is necessary to fully understand species–environment relationships. Such insights would allow recruitment assumptions in management to be grounded in underlying ecological processes, rather than solely on empirical approaches (Alewijne et al. 2025, Dunn 2025). A clearer understanding of the mechanisms through which temperature and other climate-related factors influence early life stages and recruitment will ultimately enable more informed and effective management under changing environmental conditions.

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Author contributions

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– original draft [lead], Timothy Jones (Conceptualization [lead], Formal Analysis [lead], Methodology [lead], Visualization [lead], Writing – original draft [lead]), Sally Thorpe (Conceptualization [supporting], Writing – review & editing [equal]), Jaimie Cleeland (Writing – review & editing [equal]), Timothy Earl (Writing – review & editing [equal]), Jennifer Freer (Writing – review & editing [equal]), Simeon Hill (Writing – review & editing [equal]), Oliver Hogg (Writing – review & editing [equal]), Philip Hollyman (Writing – review & editing [equal]), Claire Waluda (Writing – review & editing [equal]), Martin Collins (Conceptualization [supporting], Writing – review & editing [equal])

Supplementary data

Supplementary data are available at *ICES Journal of Marine Science* online.

Conflicts of interest

None declared.

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Data availability

The groundfish survey data are available from the UK Polar Data Centre <https://doi.org/10.5285/fd2f9f1c-bb9f-484e-bbc1-b3d20668b8d2> (Collins et al. 2026). The OSTIA and GLORYS12V1 temperature products used in this study are publicly available from the E.U. Copernicus Marine Service Information (<https://doi.org/10.48670/moi-00165>, <https://doi.org/10.48670/moi-00021>).

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