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# Estimating Patagonian toothfish (*Dissostichus eleginoides*) length at first maturity from their age, sex and temperature experience around South Georgia

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## Abstract

Patagonian toothfish (*Dissostichus eleginoides*) are a long-lived, slow-growing deep-sea species endemic to the Southern Hemisphere and the focus of longline fisheries managed to ensure sustainable exploitation. Managing the fisheries relies on accurate stock assessments that include pertinent biological and exploitation processes. Length and age at first maturity are key biological parameters used in the stock assessments for Patagonian toothfish in South Georgia (Subarea 48.3). The conventional approach to estimating length and age at first maturity relies on macroscopic gonadal staging, but this may be confounded by the difficulty in distinguishing immature and mature resting (i.e., skipped spawning) individuals. Here, we extend existing length-at-age breakpoint models to incorporate sex and individual temperature experience, while accounting for increasing variation in length with age. We fit and compare a set of candidate models to assess the empirical evidence for temperature experience effect on sex-specific length at first maturity estimates using data from 3683 Patagonian toothfish sampled by both commercial longline fisheries and scientific surveys around South Georgia between 2010 and 2023. Our analysis supports an expected non-linear effect of age on length, with a higher age at first maturity for females compared to males, and demonstrates that temperature experience explains significant variation unaccounted for by age and sex alone, showing an inverse relationship between the temperature experienced by Patagonian toothfish and their length-at-age. These findings have direct implications for improving the biological realism and predictive accuracy of stock assessment models, particularly under climate change.

KEYWORDS
change point analysis, climate change, fisheries stock assessment, length-at-age, non-constant variance, South Georgia

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## 1 | INTRODUCTION

Patagonian toothfish (*Dissostichus eleginoides* Smitt 1898) are a long-lived deep-sea nototheniid fish endemic to the southern Atlantic, Pacific and Indian oceans, as well as the Southern Ocean (Collins et al., 2010). Similar to other deep-water fish species, Patagonian toothfish are slow-growing and maturing, long-lived fish. They can reach lengths of over 2 m during a life span of at least 50 years, not reaching reproductive maturity before approximately 7–10 years of age (Collins et al., 2010). In the Subantarctic, this species is targeted by relatively small and highly regulated benthic longline fisheries, and the exploited stocks are managed in line with the Harvest Decision Rules of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), aiming for these stocks to remain around 50% of their unfished spawning stock biomass over the next 35 years (CAMLR Convention Article II; Agnew & Kirkwood, 2005; Collins et al., 2010; Hanchet et al., 2015).

Fishery management advice for Patagonian toothfish relies on regular stock assessments, which quantify numbers of Patagonian toothfish as accurately as possible, accounting for the pertinent biological processes underlying stock dynamics, as well as the exploitation processes acting on them (Quinn II & Deriso, 1999). Currently, Patagonian toothfish stocks across the Subantarctic are assessed with integrated Bayesian models (Doonan et al., 2016) that infer population dynamics from data collected in standardised tag-recapture programmes, together with biological sampling data, to estimate current, past and future spawning stock biomass under different fishing pressure scenarios. The maturity ogive, which provides an estimate of the length or age at which a fish gains the ability to reproduce, is therefore an influential part of the stock assessment models (notably, alongside individual growth rates) (e.g., Trehin et al., 2021).

At present, the maturity ogive for Patagonian toothfish is based on estimated fish age, which is derived from otolith chronologies and estimated gonad reproductive stages (hereafter *gonad stages*). Together with biological parameter data and otolith collection, gonad stages are classified macroscopically into a standardised categorisation by trained scientific observers according to visual cues using standardised data collection methods developed on long-term historical records from across the CAMLR Convention Area [CCAMLR Scheme of International Scientific Observation (CCAMLR SISO), 2025; Gasco et al., 2011; Table 1]. Although this approach leverages historical information, standardisation and expert opinion, it also represents only a simplified generalisation of Patagonian toothfish reproductive cycles.

Recent evidence suggests that Patagonian toothfish females around South Georgia spawn in two peak periods (Bamford et al., 2024) but with oocyte maturation occurring only once per year (Amthauer et al., 2021) and that a non-trivial proportion of females do not spawn in each cycle, skipping spawning under certain conditions (Boucher, 2018; Everson & Murray, 1999). However, using macroscopical staging to distinguish between gonads of a sexually immature individual and those of resting or non-reproducing gonads in a sexually mature individual can be challenging in Patagonian toothfish (Gasco et al., 2011; Yates et al., 2018), and both are categorised as ‘2 – maturing virgin or resting’ within the CCAMLR data collection (Table 1). A study comparing macroscopic versus histological maturity

**TABLE 1** Gonadal staging of Patagonian toothfish, as assigned by macroscopic inspection.

| Sex | Gonadal stage | Description |
|---|---|---|
| Female | 1 | *Immature*: Gonad oval in shape, translucent with smooth exterior. Ovary small, firm, no eggs visible to the naked eye. Very small in size, taking up little of the visceral cavity. |
| | 2 | *Maturing virgin or resting*: Ovary more extended, firm, small white oocytes visible, giving ovary a grainy appearance. Generally pale pinkish in colour. Small in size, taking up less than half of the visceral cavity. |
| | 3 | *Developing*: Gonads smooth with many eggs which are clearly visible through the gonad wall. Ovary large, starting to swell the body cavity, colour varies according to species, contains oocytes of two sizes. Medium size gonads occupying about half of the visceral cavity. |
| | 4 | *Gravid*: Ovary large, filling or swelling the body cavity, when opened large ova spill out. Pressure on the abdomen causes ova to be released. All ova are formed. Very large gonads filling most of the visceral cavity. |
| | 5 | *Spent*: Ovary shrunken, flaccid, contains a few residual eggs and many small ova. Ovary wall thick and leathery, often with signs of blood or bruising. Gonad size approximately a third of the visceral cavity. |
| Male | 1 | *Immature*: Testis small, translucent, whitish, long, thin strips lying close to the vertebral column. Very small in size taking up little of the visceral cavity. |
| | 2 | *Developing or resting*: Testis white, flat, convoluted, easily visible to the naked eye, about 1/4 length of the body cavity. Generally pink in colour. |
| | 3 | *Developed*: Testis large, white and convoluted, no milt produced when pressed or cut. Generally pinkish in colour. Gonads occupy a large part of the visceral cavity. |
| | 4 | *Ripe*: Testis large, opalescent white, drops of milt produced when pressed or cut. Gonads occupy most of the visceral cavity. |
| | 5 | *Spent*: Testis shrunk, flabby, dirty white in colour. Firm texture. When cut, milt remnant can be seen in the tissue. Gonads occupy a third of the visceral cavity. |

*Source*: From Kock and Kellermann (1991), Gasco et al. (2011) and CCAMLR SISO (2025).

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staging in Patagonian toothfish found 65% and 26% of females classified macroscopically as stage 2 ('maturing virgin or resting') and stage 1 ('immature'), respectively, exhibited histological evidence of past spawning and/or oocyte development, suggesting individuals were, in fact, sexually mature (Yates et al., 2018). Using macroscopic stages for estimating the age at which maturity first occurs in females (age at first maturity) can therefore introduce an element of uncertainty.

Without detail on first maturation readily available from current data collection, age at first maturity must be estimated based on proxy information, such as length-at-age. Reliable length-maturity keys are a useful representation for understanding reproductive dynamics in a population over time. However, as mature female Patagonian toothfish that skip spawning can skew this relationship towards larger sizes, this can result in uncertainty when determining the length or age at first maturity in a population, and introduce inaccuracies to length-maturity keys (Everson & Murray, 1999). To resolve this 'Catch-22' problem, past analyses have used empiric length-at-maturity tables to distinguish among fishes that are likely or unlikely to have become sexually mature (Everson & Murray, 1999).

An alternative approach to estimating length or age at first maturity is the use of length-at-age models that use breakpoints in this relationship (Scott & Heikkonen, 2012). Such models use the fact that fish show indeterminate growth, which means that they grow throughout their lifetime, and so age is strongly related to their size, for example, body length (Marsh, Cove, et al., 2022; von Bertalanffy, 1957). Breakpoints in the age–length relationship can represent the point at which metabolic resources are first redirected from somatic to reproductive growth, that is, the age at first maturity (Scott & Heikkonen, 2012).

Age is not the sole influence on the length a fish attains and temperature has been found consistently to influence fish growth rate (e.g., Marsh, Cove, et al., 2022), even in the deep sea where temperatures are somewhat isothermic (Thresher et al., 2007). An organism's biological performance (including growth) is expected to follow a thermal performance curve (Schulte, 2015), increasing with temperature to their optimum and then rapidly decreasing (termed the pejus temperature; Farrell, 2016). To date, very little is known on how temperature influences growth in toothfish. An inverse lagged relationship between growth and temperature was found in juvenile Patagonian toothfish: The average length of juvenile toothfish was greater following cooler sea-surface temperatures during the summer prior to spawning, which was attributed to improved feeding conditions (Belchier & Collins, 2008). Although growth parameters are described for assessing stocks of toothfish populations throughout the CAMLR Convention Area and beyond (and thus a range of temperature conditions, i.e., CCAMLR Secretariat, 2025; Earl et al., 2023; Massiot-Granier et al., 2023a; Skeljo, 2025), direct comparisons of growth between populations are difficult as fishing methods differ, and so these observations are also influenced by fishery selectivity (see also Yates et al., 2018). In recognition of the importance of biological change to stock assessments, key parameters (including growth) are reviewed during each toothfish assessment in the CAMLR Convention Area for evidence of change due to environmental variability (e.g., Earl et al., 2023).

In this paper, we examine whether an extended length-at-age model can produce objective estimates of length and age at first maturity estimation for Patagonian toothfish, using data from fish caught around South Georgia (FAO Subarea 48.3) in the Atlantic Southern Ocean. We extend a model presented by Scott and Heikkonen (2012), which they used to investigate the length at first maturity among female and male plaice *Pleuronectes platessa* in the Irish Sea, to include the sex and temperatures experienced by individual fish during its lifetime. We include sex-specific parameters to account for observed differences in length-at-age and age at maturity in Patagonian toothfish, that is, females mature at later ages and are larger for a given age than males (e.g., Marsh, Earl, et al., 2022). We fit and compare a set of a priori chosen candidate models to sex-specific length data to assess the empirical evidence for our hypotheses about the influences of age, sex and temperature experience on their length at first maturity. We predict that age will be non-linearly related to length, with a sex-specific breakpoint representing age at first maturity that is higher for females compared with males, and that inclusion of temperature experience will explain a non-negligible amount of variation in length that is unexplained by age and sex alone.

## 2 | MATERIALS AND METHODS

### 2.1 | Data

Patagonian toothfish were sampled from Subarea 48.3 (Figure 1a) in both the licensed commercial longline fishery and scientific groundfish surveys. Data from the commercial longline fishery ($n = 3556$ individuals) were obtained from UK fishing vessels in the 2010 to 2023 fishing seasons. These data were obtained from CCAMLR Data Request 747. Longlines were set at depths between 526 and 1964 m (mean depth 1277 m); as such these data contain few records of immature individuals, which are benthopelagic and occupy shallower depths (<250 m; Belchier & Collins, 2008; Earl et al., 2023). To ensure inclusion of immature individuals, data from the 2015 and 2021 South Georgia biennial random stratified bottom trawl groundfish survey were also included ($n = 127$ individuals), with fishing depths ranging from 50 to 350 m, and 100 to 350 m, respectively, and using a commercial otter trawl towed at three knots for 30 min (Belchier et al., 2015). In both the fishery and surveys, onboard fisheries observers and scientists measured a subset of Patagonian toothfish for total length (mm), and recorded sex and gonadal stage on a five-point scale (CCAMLR SISO, 2025; Kock & Kellermann, 1991; Figure 1b, Table 1).

Sagittal otolith pairs were removed from Patagonian toothfish selected randomly during longline fishing operations and research trawls during biological data collection outlined above. For age determination, otoliths sourced from commercial longlines were stratified by total body length and sex. Specifically, otoliths from four male and four female fish were randomly selected from each 1-cm size class present. Otoliths from the groundfish survey were sampled in a similar

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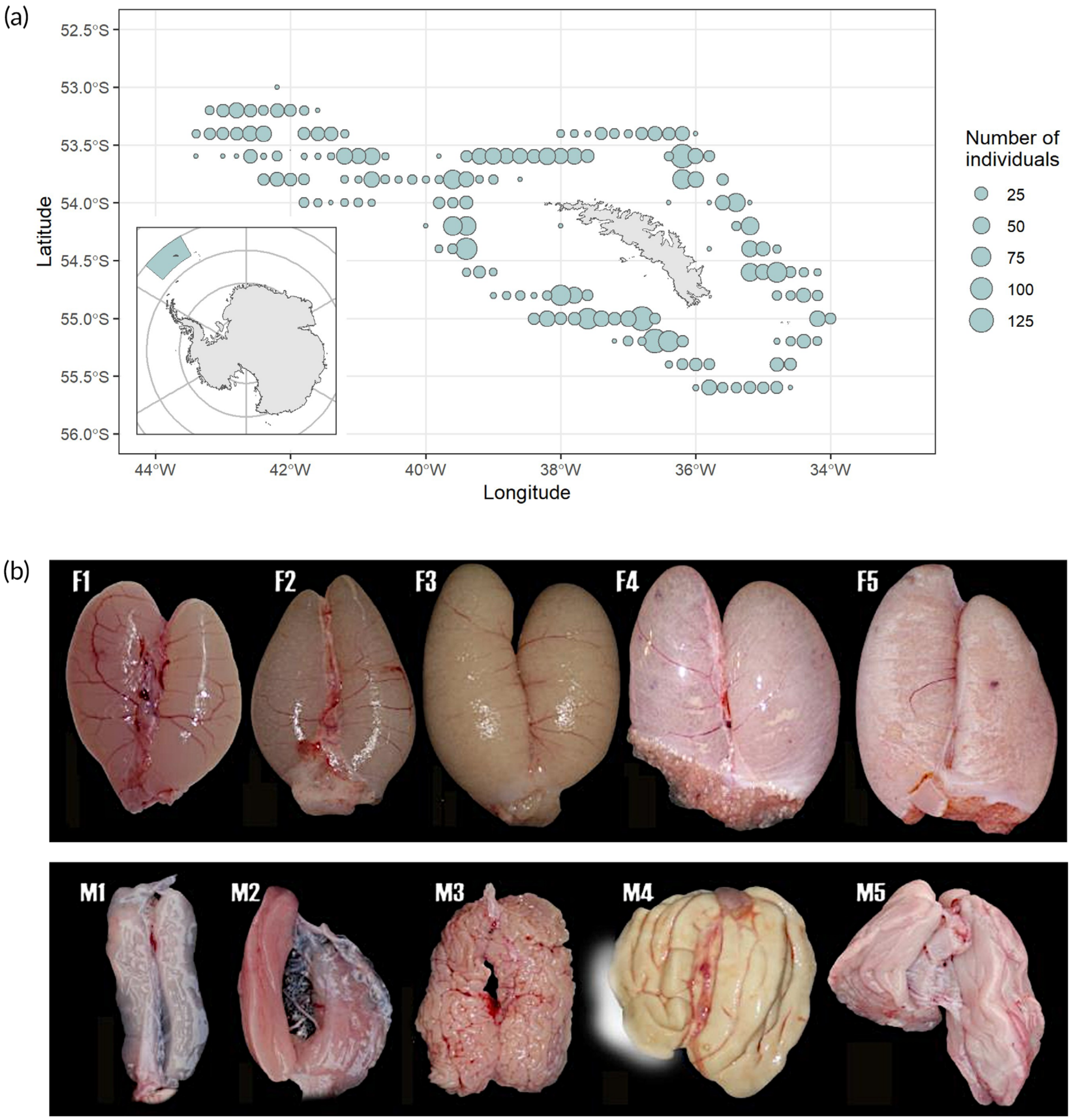

**FIGURE 1** Panels showing (a) a map of South Georgia FAO Subarea 48.3 showing the approximate location and numbers of Patagonian toothfish individuals used in this study, and (b) a plate showing examples of female (F) and male (M) gonad stages from the CCAMLR SISO Manual (1:5; see also Table 1; reproduced with permission by N. Gasco). GIS data from the UK Polar Data Centre, accessed using the CCAMLRGIS R package (Thanassekos et al., 2025).

way for 2021, although five individuals per 1-cm size class were processed. All otoliths collected on the 2015 survey were analysed. The left otolith from each selected pair was embedded in clear epoxy casting resin (ABL Resin & Glass). Transverse thin sections of each otolith were produced using a Struers Minitom precision saw (~600 μm thick). Thin sections were then mounted on a standard microscope slide with a glass cover slip using more resin and left to cure. Ages of each otolith were then estimated by experienced readers by counting annuli (paired translucent and opaque zones) from the central nucleus to the edge at 20× magnification using an Olympus BX-50 compound microscope. The readability of each sample was scored 1–5 (with decreasing confidence); any samples scoring a 5 (unreadable) were removed from the age dataset.

Data on monthly mean bottom temperature at the Patagonian toothfish catch locations were downloaded from Copernicus (variable *sea water potential temperature at the seafloor*; CMEMS, 2025). As these data are available only from 1993, we subset the toothfish records to those individuals estimated to have been spawned in or after 1993 by subtracting their age from their date of capture. These data were then used to calculate degree month anomalies, a measure of the temperature experienced in an individual's lifetime.

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**TABLE 2** Candidate models for testing for breakpoints in sex-specific length-age relationships of Patagonian toothfish and effects of temperature experienced, represented as degree month anomalies or the sum of monthly mean temperatures between dates of hatch and capture conditioned by age (in months).

| Model | Terms | Equation | Testing | Hypothesis | References |
|---|---|---|---|---|---|
| M0 | Length ∼ sex + age | $y_i = \alpha + \beta_{S_i} + \beta_A A_i$ | Sex-specific length-age relationship (null model) | Length-at-age differs by sex; females are larger for a given age relative to males | Marsh, Earl, et al. (2022), Pauly (2019) |
| M1 | Length ∼ sex + sex-specific breakpoint on age | $y_i = \alpha + \beta_{S_i} + \beta_{A_1}(A_i - \delta_{S_i}) + \beta_{A_2}\sqrt{(A_i - \delta_{S_i})^2 + \gamma}$ | Sex-specific length-age relationship including a sex-specific breakpoint representing maturity | As M0, plus fish grow quicker before maturity than after maturity, and the point of first maturity is later in females than in males | von Bertalanffy (1957) |
| M2 | Length ∼ sex + age + degree month anomalies | $y_i = \alpha + \beta_{S_i} + \beta_A A_i + \beta_{\mathrm{dm}} \mathrm{dm}'_i$ | Sex-specific length-age relationship including an effect of temperature experienced | As M0, plus fish attain greater length in cooler temperatures | Belchier and Collins (2008) |
| M3 | Length ∼ sex + sex-specific breakpoint on age + degree month anomalies | $y_i = \alpha + \beta_{S_i} + \beta_{A_1}(A_i - \delta_{S_i}) + \beta_{A_2}\sqrt{(A_i - \delta_{S_i})^2 + \gamma} + \beta_{\mathrm{dm}} \mathrm{dm}'_i$ | Sex-specific length-age relationship including a sex-specific breakpoint representing maturity and an effect of temperature experienced | As M1, plus fish attain greater lengths in cooler temperatures | As above |

Degree months for an individual ($\mathrm{dm}_i$) were calculated as follows:

$$\mathrm{dm}_i = \sum_{t=H_i}^{C_i} t, t > 0$$

where $C_i$ is the month of the date that individual $i$ was caught, $H_i$ is the month of the hatch date and $t$ is the mean monthly bottom temperature in degrees Celsius, limited to be only those greater than 0 since toothfish were not expected to grow below this temperature. To calculate hatch date, age (in months) was subtracted from the date the fish was caught and rounded to the nearest 1st of July. July was chosen because this month corresponds with a major peak in spawning activity of Patagonian toothfish in this area (Bamford et al., 2024) To remove the influence of older individuals that will have almost certainly passed their first maturity, we subset data to remove individuals of age >360 months (30 years). Degree months is analogous to the more widespread measure of degree days except that it is the sum of monthly mean temperatures rather than daily mean temperatures; we considered monthly mean temperatures as a good representation of past temperature experience because (1) bottom temperatures at this latitude are somewhat isothermic with low day-to-day variability and (2) fishing generally occurred between May and September each year (Collins et al., 2021), such that an annual timeframe that omitted temperatures experienced between the dates of capture and hatch was considered too coarse. To calculate degree month anomalies ($\mathrm{dm}'_i$), age was subtracted from degree months.

## 2.2 | Length-at-age models

The relationship between length and age was modelled using the alternative parameterisation of the two-stage breakpoint model presented in Scott and Heikkonen (2012) that takes the form:

$$y_i = \alpha + \beta_{A_1}(A_i - \delta) + \beta_{A_2}\sqrt{(A_i - \delta)^2 + \gamma} + \epsilon_i^*$$

where $y_i$ is the length of an individual (in mm), $A_i$ is the age of an individual (in months), $\alpha$ is a constant intercept, $\beta_{A_1}$ and $\beta_{A_2}$ are the effects of age on length before and after the breakpoint $\delta$, respectively, $\gamma$ controls the breakpoint curvature and $\epsilon_i^*$ is a residual for individual $i$ that captures the model lack-of-fit and is weighted by their age to account for an observed increasing variation in length with increasing age.

The Scott and Heikkonen model was expanded to a candidate model set to test a priori hypotheses about Patagonian toothfish length at first maturity developed from the literature and exploratory analysis of the data (Table 2). Specifically, the comparison among models in the candidate model set was designed to reveal empirical evidence for the existence of a change point in the relationship between length and age and, if present, to test whether it differed between sexes and was affected by degree month anomalies.

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**TABLE 3** Notation used to describe candidate models explored in this study, including prior specification on model parameters.

| Notation | Description | Prior |
|---|---|---|
| $y_i$ | Total length (mm) of individual *i* | - |
| $\alpha$ | Intercept | $\mathrm{Normal}(0, 1000)$ |
| $\beta_{S_i}$ | Effect of individual *i*'s sex (1 = female, 2 = male) on length, with $\beta_{S_1}$ fixed to 0 as the contrast level | $\mathrm{Normal}(0, 1000)$ |
| $\beta_A$ | Effect of age on length | $\mathrm{Normal}(0, 1000)$ |
| $\beta_{A_1}$ | Effect of age on length before the breakpoint | |
| $\beta_{A_2}$ | Effect of age on length after the breakpoint | |
| $A_i$ | Age (months) of individual *i* | - |
| $\delta_{S_i}$ | Sex-specific breakpoint (1 = female, 2 = male) | $\mathrm{Uniform}(\mathrm{minage}, \mathrm{maxage})$ |
| $\gamma$ | Curvature of the breakpoint | $\mathrm{Half}-\mathrm{Normal}(0, 1000)$ |
| $\beta_{\mathrm{dm}}$ | Effect of degree month anomalies on length | $\mathrm{Normal}(0, 1000)$ |
| $\mathrm{dm}'_i$ | Degree months anomalies for individual *i* | - |
| $\sigma$ | Standard deviation of model error weighted by age, that is, $\sigma \times A$ | $\mathrm{Student}-t_{(\mathrm{df}=1)}(0, 1000) \approx \mathrm{Half}-\mathrm{Cauchy}$ |

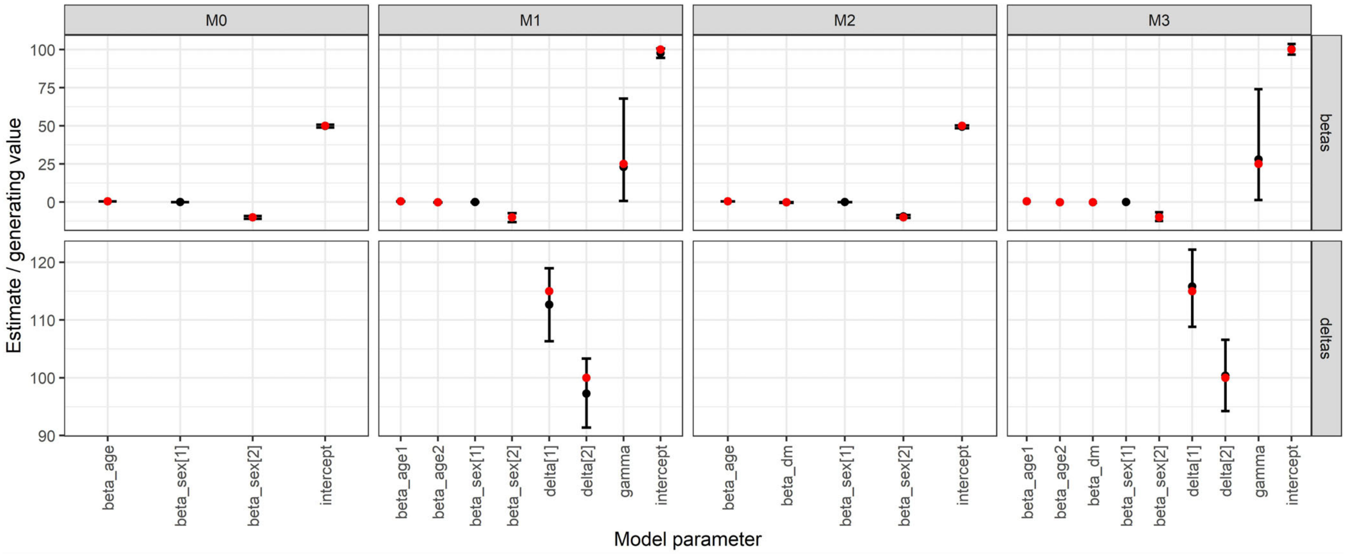

**FIGURE 2** Panels showing estimated (black points and uncertainty bars) compared to generating (red points) parameter values for each model from an example of the simulation testing, where female = 1 and male = 2 for the beta_sex and delta model parameters.

To confirm our understanding of the models and ensure parameter identifiability, we tested the ability of each model to recover the values of model parameters used to generate datasets simulated from it, that is, simulation testing. Each simulated dataset was designed with characteristics of our observed Patagonian toothfish dataset with respect to number of observations, lengths, ages and degree month anomalies.

All model parameter values were estimated from parallel Markov Chain Monte Carlo (MCMC) chains sampled using the Gibbs sampler in JAGS (Plummer, 2023) called by the R2jags package (Su & Yajima, 2024) from R version 4.4.1 (R Core Team, 2024). We assigned weakly informative priors to all model parameters (Table 3). Models were run in three chains for 100,000 iterations, using a burn-in period of 50,000 iterations and a thinning parameter of 100. All models were checked for convergence via visual inspection of chains, posterior densities and autocorrelation function plots (see Supporting Information), as well as the Gelman-Rubin diagnostic (R-hat). Models were compared using leave-one-out (LOO) cross-validation information criterion implemented in R package loo (Vehtari et al., 2024) to identify the model best describing the data for inference.

## 3 | RESULTS

### 3.1 | Simulation testing

Each model was explored using simulation testing and was found to recover the values of parameters used to generate simulated datasets

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**TABLE 4** Model comparison using leave-one-out (LOO) information criterion, with both expected log pointwise predictive density (ELPD) and standard error (SE).

| Model | LOO ELPD | LOO SE | ΔLOO ELPD | ΔLOO SE |
|---|---|---|---|---|
| M3 | −14,318.7 | 52.9 | - | - |
| M1 | −14,334.2 | 53.0 | −15.5 | 6.5 |
| M2 | −14,728.2 | 52.5 | −409.5 | 32.6 |
| M0 | −14,745.4 | 52.0 | −426.6 | 32.6 |

*Note*: Models are ordered with the model best describing the data at the top.

from it (Figure 2). An example of the simulation testing is given at https://github.com/CefasRepRes/alewijnse-top-length-at-maturity. These simulations reassured us that the models were identifiable despite some correlation between the posterior of sex-specific breakpoints, intercept, and age effect estimates.

## 3.2 | Models

Visual and statistical diagnostics suggested that all model parameter estimates were inferred from well-mixing parallel MCMC chains (Table S1; Figures S1–S3).

### 3.2.1 | Model comparison

According to the LOO cross-validation (Table 4), model M3 best described the observed Patagonian toothfish lengths and included their temperature experiences (measured as degree month anomalies) alongside a sex-specific breakpoint in their age and an overall effect of sex.

### 3.2.2 | Model inference

From the best model M3 fit (Figure 3) and parameter estimates (Table 5), we could infer that (1) being male ($\beta_{S_2}$) had a relative negative effect on length, indicating that males are smaller than females at a given age; (2) the effect of age before the breakpoint ($\beta_{A_1}$) was positive, indicating that length increases with age, at least up to the breakpoint that was taken to represent maturity; (3) the effect of age after the breakpoint ($\beta_{A_2}$) was negative, indicating that growth slows after the breakpoint; (4) that the breakpoint occurs earlier in males ($\delta_{S_1}$) than in females ($\delta_{S_2}$), indicating that males mature earlier than females; and (5) the effect of degree days ($\beta_{\mathrm{dm}}$) was negative, indicating that exposure to higher temperatures during their lifetime results in shorter lengths at a given age, sex and maturity status. Reassuringly, these inferences did not differ for simpler models, that is, the parameter estimates were similar between models (Table 5).

While the positive effect of age on length is widely understood (i.e., fish growth is indeterminate), the effect of temperature experience is rarely considered alongside age (with or without a breakpoint). For Patagonian toothfish, these data and model comparisons suggest that individuals exposed to higher temperatures over their lifetime attained shorter lengths at a given age compared to individuals exposed to lower temperatures over their lifetime (Figure 4).

### 3.2.3 | Comparison of age at maturity

Taking the breakpoints ($\delta$) as an estimate of age at 50% maturity gives mean estimates of 13.9 years for females, and 9.1 years for males. By comparison, 47% of females and 43% of males below these ages were identified as having immature gonads using macroscopic staging (stage 1), rising to 77% and 68% when adding in mature virgin or resting (stage 2) females and males, respectively.

Compared with a recent stock assessment for Patagonian toothfish in Subarea 48.3 for which estimated age at 50% maturity was based on macroscopic gonadal staging (in which maturity was defined as stages 2–5; Earl et al., 2023; Earl & Readdy, 2023), the results of this study suggest a higher age at 50% maturity for both sexes (Table 6). Both methods estimate a relatively large difference in age at 50% maturity between females and males.

# 4 | DISCUSSION

## 4.1 | Extension of the Scott and Heikkonen model

This work presents a novel extension to the Scott and Heikkonen (2012) model, wherein the length at first maturity can be determined by a breakpoint in the length-at-age model. Slowing of growth with increasing size after this breakpoint shows an allocation of energy away from somatic growth. This phenomenon is well known in fish (von Bertalanffy, 1957) and is reflected in stock assessment models by assuming non-linear growth models, such as the von Bertalanffy growth function (Earl et al., 2023; Earl & Readdy, 2023). Furthermore, this work suggests that the identified sex-specific breakpoints correspond reasonably well with macroscopic observation of individual maturation, providing evidence that the breakpoint models capture the additional cost of reproduction and associated reduced growth rate after reaching maturity in Patagonian toothfish (Horn, 2002; Marsh, Earl, et al., 2022; Soeffker et al., 2022).

Secondly, a well-known aspect of fish physiology is the difference in growth and maturity between female and male fish. Female fish tend to grow to larger sizes than their male conspecifics (Pauly, 2019), and female Patagonian toothfish have been noted to mature later than males (Alewijnse & Earl, 2025; Marsh, Earl, et al., 2022). The former is reflected in the von Bertalanffy growth function, with female Patagonian toothfish having greater asymptotic lengths ($L_\infty$) and smaller Brody growth coefficients ($K$, Earl et al., 2023; Earl & Readdy, 2023). In all models tested in this study, males were smaller than females at the same age, consistent with established fish physiology and previous observations of Patagonian toothfish across their

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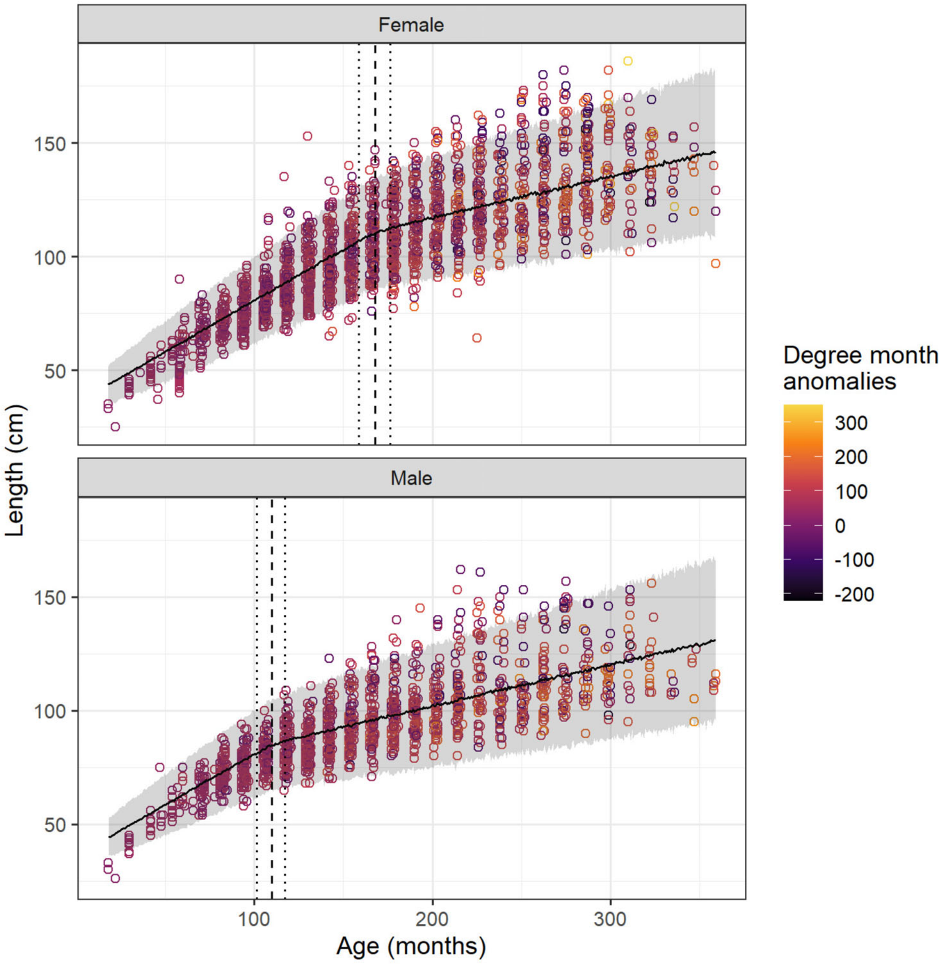

**FIGURE 3** Relationship between age (months) and length (cm) of Patagonian toothfish (*Dissostichus eleginoides*) around South Georgia (Subarea 48.3). The fitted model is M3, with mean length-at-age predictions shown using the black line (grey ribbon indicating 95% credible intervals) and mean break point prediction shown using the vertical dashed line (dotted lines indicating 95% credible intervals). Degree month anomalies represent a measure of the temperature experienced in an individual's lifetime, calculated as the degree months subtracted from the individual age in months.

range (e.g., Ross Sea, Horn, 2002; Kerguelen Plateau, Welsford et al., 2011; South Georgia and South Sandwich Islands, Soeffker et al., 2022). Similarly, the later breakpoints in the length-at-age relationships in female Patagonian toothfish compared to males reflects their later age and size at maturity (Collins et al., 2010). The alignment between established aspects of fish physiology and the best model fits supports the use of the extended Scott & Heikkonen model for estimating age at first maturity in Patagonian toothfish.

Our findings provide the missing detail of first maturation in Patagonian toothfish that could not be readily captured in current data collection. The extended Scott and Heikkonen model employed here offers a means of estimating length and age at maturity, independent of macroscopic gonadal staging. While results were similar, there was some difference between the two methods, with the breakpoint model predicting older ages at 50% maturity than macroscopic gonadal staging, particularly for females. Such differences could arise depending on whether stage 2 samples are included as immature or mature fish. The stock assessment currently assumes that only stage 1 individuals are immature (Earl et al., 2023; Earl & Readdy, 2023), which may account for the differences between estimates of age at 50% maturity between macroscopic gonadal staging and the breakpoint model. Nonetheless, the relative similarity in estimates from both methods lends confidence to each and supports the values used in the stock assessment. Furthermore, age at 50% maturity estimates produced in this study are broadly consistent with those derived from alternative methods on other Patagonian toothfish populations, for example, using the gonado-somatic index (GSI) and microscopic gonad evaluation in the Kerguelen Plateau toothfish population (Yates et al., 2018).

Additional microscopic gonad evaluation would provide definitive data to elucidate the timescale of maturation (e.g., Yates et al., 2018). However, this is also a resource intensive approach requiring significant additional data collection and sample processing. The Scott and Heikkonen approach used in our study makes effective use of existing data to estimate age at maturity independent of gonadal staging. Having demonstrated this ability, this modelling approach could usefully be applied to other fisheries or surveys which have similar data available.

## 4.2 | Effect of temperature on growth

In our study, there was an inverse relationship between the temperature experienced by Patagonian toothfish (as degree month anomalies) and their length-at-age. This aligns with previous findings that, in Patagonian toothfish in Subarea 48.3, if the summer prior to spawning

**TABLE 5** Parameter estimates from candidate models.

| Model | Parameter $\alpha$ | $\beta_{S_2}$ | $\beta_A$ $\beta_{A_1}$ | $\beta_{A_2}$ | $\beta_{dm}$ | $\delta_{S_1}$ | $\delta_{S_2}$ | $\gamma$ | $\sigma$ |
|---|---|---|---|---|---|---|---|---|---|
| M3 | 111.976 ± 1.784 | −27.724 ± 1.394 | 0.352 ± 0.007 | −0.135 ± 0.005 | −0.021 ± 0.004 | 167.739 ± 4.749 | 109.752 ± 3.912 | 51.428 ± 25.237 | 0.966 ± 0.011 |
| M1 | 110.124 ± 1.741 | −27.658 ± 1.366 | 0.350 ± 0.007 | −0.136 ± 0.005 |  | 166.124 ± 4.725 | 107.944 ± 3.869 | 51.635 ± 24.554 | 0.970 ± 0.012 |
| M2 | 45.761 ± 0.502 | −5.557 ± 0.416 | 0.342 ± 0.003 |  | −0.024 ± 0.004 |  |  |  | 1.081 ± 0.013 |
| M0 | 45.077 ± 0.505 | −5.715 ± 0.408 | 0.337 ± 0.003 |  |  |  |  |  | 1.086 ± 0.013 |

*Note*: Blank columns indicate that parameters are not present within that model. Models are ordered by their leave-one-out (LOO) estimate given in Table 4.

was cooler, then the resulting cohort of juvenile fish had an average greater length than in warmer summers prior to spawning (Belchier & Collins, 2008). Additionally, a comparison of growth rates between Patagonian toothfish caught in Subarea 48.3 and those caught in the more southerly South Sandwich Islands (Subarea 48.4) showed Patagonian toothfish in Subarea 48.4 to grow faster and attain larger length-at-age (Soeffker et al., 2022). These studies therefore suggest that cooler temperatures can confer faster growth rates on Patagonian toothfish within the South Georgia-South Sandwich Islands population, although neither study provides an unequivocal mechanism, for example, temperature acting directly on metabolism or indirectly via food availability, discussed below. We note that larger body size at cooler temperatures has been postulated as a general phenomenon (i.e., Bergmann's rule; Bergmann, 1848) for endotherms, but its applicability to ectotherms is still debated (e.g., Zamora-Camacho et al., 2014). Our study demonstrates further evidence of its applicability to a high-latitude fish species, concurrent with observations in mesopelagic fish communities in the Southern Ocean (Saunders & Tarling, 2018).

The exact mechanisms underlying this observed temperature influence remain unclear and several hypotheses are plausible. Cooler water temperatures can be associated with favourable environmental conditions that promote growth opportunities. For example, observations of other fish species confirmed that higher dissolved oxygen (and associated aerobic scope) in cooler waters may be a factor contributing to faster growth rates in lower water temperatures (Farrell, 2016). Patagonian toothfish may have metabolic rates closer to active large temperate fish species with fast growth rates such as cod (e.g., *Gadus morhua*) or trout (e.g., *Salmo trutta*), rather than deep-sea species with slow metabolisms (Encina-Montoya et al., 2024). These observations were made in warmer surface waters and in captive fish, and so the expected impact of pressure at depth on metabolic rate could not be measured. Nevertheless, this first glimpse at the metabolism of this species could potentially explain why Patagonian toothfish grow slower in warmer waters.

Higher water temperatures may also be associated with lower productivity. Consequently, fish inhabiting warmer waters could experience periods of food limitation during their life history, ultimately resulting in reduced growth compared to individuals living in colder, more productive environments. Belchier and Collins (2008) suggested that the inverse relationship between temperature and average juvenile length in Patagonian toothfish could be related to productivity driven by krill. Krill recruitment is typically higher in cooler periods (Murphy et al., 2006), and while krill themselves are form a small part of juvenile toothfish diets (Collins et al., 2007), the 'bottom up' control driven by krill abundance could impact toothfish growth (Belchier & Collins, 2008). Lastly, localised adaptation could also play a role. Patagonian toothfish in Subarea 48.3 are close to their lower temperature range edge in 48.3, but highly unlikely to be living at the upper end of the species' thermal tolerance (Collins et al., 2010; Encina-Montoya et al., 2024). The South Georgia-South Sandwich Islands toothfish population are genetically distinct from other Patagonian toothfish populations (Arkhipkin et al., 2022; Canales-Aguirre

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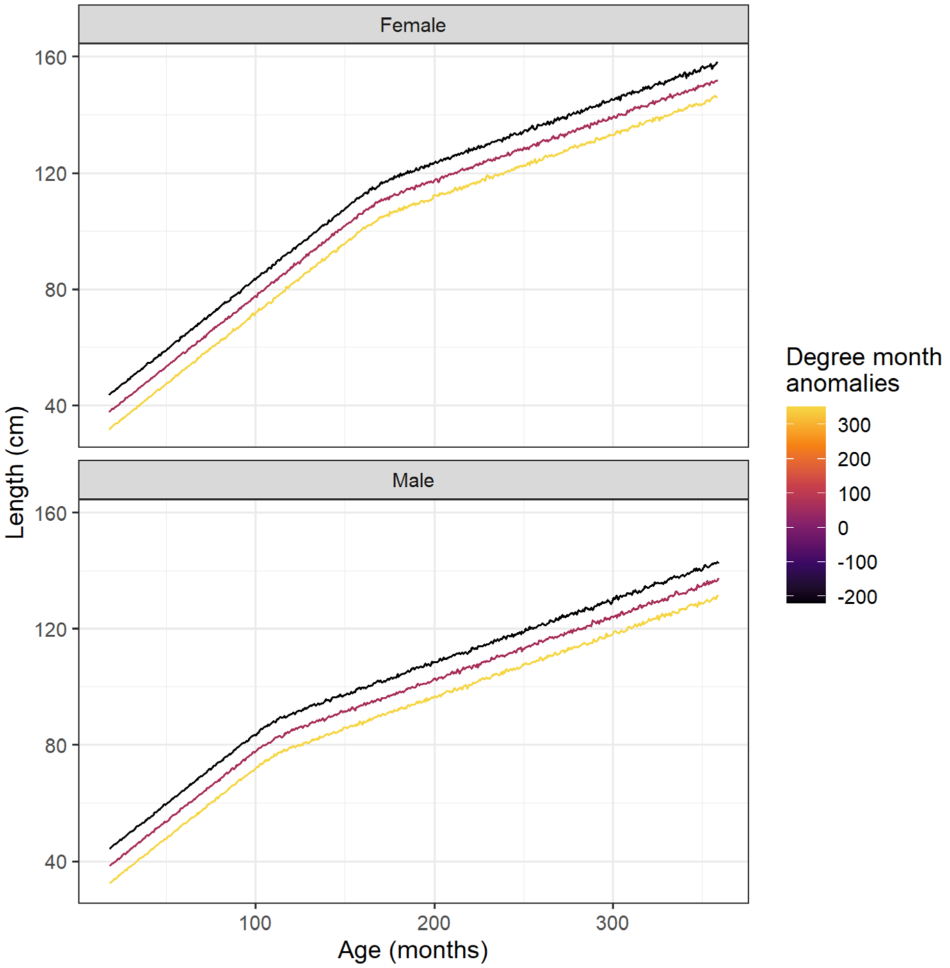

**FIGURE 4** Predictions of length-at-age for Patagonian toothfish (*Dissostichus eleginoides*) using model M3 at minimum (black), mean (red) and maximum (yellow) degree month anomalies. Degree month anomalies represent a measure of the temperature experienced in an individual's lifetime, calculated as the degree months subtracted from the individual age in months.

**TABLE 6** Comparison of age at 50% maturity reported in the 2023 Stock Annex for Subarea 48.3 Patagonian toothfish (Earl et al., 2023; Earl & Readdy, 2023) to those estimated in this study based on 95% credible intervals for breakpoints ($\delta$).

| Sex | 2023 Stock Annex | This study |
|---|---|---|
| Females | 8.5–11.5 | 13.2–14.7 |
| Males | 7.0–8.2 | 8.5–9.8 |

et al., 2018; Rogers et al., 2006; Shaw et al., 2004; Toomey et al., 2016), and it is possible that this population may be specifically adapted to lower temperatures, such that they have a lower pejus temperature than other populations of the same species. Discerning among these plausible alternative mechanisms could be the subject of future work.

Sampling biases resulting from targeted fisheries with different fishing methods makes the comparison of the impact of temperature on growth rates among Patagonian toothfish populations difficult. However, comparing von Bertalanffy growth parameters among populations might offer some insight into how temperature affects growth in Patagonian toothfish at the species level. Populations from more southern latitudes have smaller observed asymptotic growth lengths than those caught further north [listed south to north: South Georgia $L_\infty = 154$ cm (Earl et al., 2023); Heard Island and McDonald Island $L_\infty = 141$ cm (CCAMLR Secretariat, 2025); Falkland Islands $L_\infty = 178$ cm (Skeljo, 2025); Kerguelen Islands $L_\infty = 170$ cm (Massiot-Granier et al., 2023a); Crozet Islands $L_\infty = 197$ cm (Massiot-Granier et al., 2023b)]. This appears to initially contrast with our results, however, which showed that colder temperatures can confer larger size at age within the same population. The observed gradient from larger to smaller asymptotic growth length across different populations caught from warmer to cooler waters could be indicative of the effect likely being population-specific in Patagonian toothfish, potentially tied to the restricted genetic exchange between populations (Arkhipkin et al., 2022; Canales-Aguirre et al., 2018; Rogers et al., 2006; Shaw et al., 2004; Toomey et al., 2016). Further work could, therefore, look to expand this study across and within different populations of Patagonian toothfish.

The Southern Ocean is warming (Atkinson et al., 2019; Turner et al., 2014; Whitehouse et al., 2008). Given the inverse relationship seen here between length-at-age and temperature, warming of Subarea 48.3 could lead to smaller individual Patagonian toothfish at a given age over time, as has been observed across taxa (Sheridan & Bickford, 2011). Alongside the direct effect of increasing temperature on Patagonian toothfish sizes, large-scale studies have shown potential subsequent effects on fish stock dynamics (Cheung et al., 2013).

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For Patagonian toothfish, recruitment is expected to be linked to spawning stock biomass (the biomass of reproducing fish in a season) via the Beverton-Holt relationship (Beverton & Holt, 1957), which is assumed in their stock assessment. In addition to the effects of a reduced biomass, larger individuals, particularly females, are the most fecund and therefore make an important contribution to recruitment (Hixon et al., 2014). Reduced length-at-age therefore has the potential to reduce spawning stock biomass and recruitment, suggesting it deserves additional consideration in the stock assessment. Finally, while adult toothfish have few predators (Collins et al., 2010), juvenile toothfish are vulnerable to predation, particularly due to their small size. Remaining at a smaller size for longer, due to a lower growth rate, may increase the opportunity for predation (Bailey & Duffy-Anderson, 2009) and thereby increase mortality during this crucial life stage.

### 4.3 | Limitations and extensions

Although the CMEMS (2025) modelled temperature at the sea bottom product allowed us to represent individual Patagonian toothfish temperature experiences since 1993, we would like to have considered temperature changes over a longer period. Several studies have suggested that deep-sea water temperatures have changed over time (e.g., Atkinson et al., 2019; Turner et al., 2014; Whitehouse et al., 2008). The time period considered here was, perhaps, insufficient to capture such changes; we believe an extension of this work including temperature experiences extending back to the hatching of the oldest Patagonian toothfish from among the earliest fishing records (i.e., temperature data back to circa 1970, perhaps inferred from sea-surface temperature data or from temperature data now collected by the longline fisheries) could provide insight into the longer-term changes in their lengths at age and length at first maturity (as has been done for age at 50% maturity; Yates et al., 2018), which could allow us to consider their recent population dynamics within a longer timeframe.

Similarly, extending this analysis to a larger spatial domain could also provide much-needed information to broaden our understanding of water temperature effects on toothfish growth and maturity, and whether the within-population temperature-growth relationship found here also holds true in other populations. Given that the population at South Georgia is genetically distinct from other Patagonian toothfish populations (Arkhipkin et al., 2022; Canales-Aguirre et al., 2018; Rogers et al., 2006; Shaw et al., 2004; Toomey et al., 2016), and at the southern end of their species range (Collins et al., 2010), the relationship between temperature and growth found here may vary from that seen in different populations.

A further extension of this study could apply this approach to another toothfish species, the Antarctic toothfish (*Dissostichus mawsoni*) to understand better the role of temperature on length-at-age and maturity in this species, which is also commercially exploited. Antarctic toothfish inhabit colder, more southerly waters and are thought to attain larger sizes compared with Patagonian toothfish (Horn, 2002). In the adjacent South Sandwich Islands, Antarctic toothfish caught in the southern region were heavier at the same length than those caught at their northern range edge, although whether this is caused by the metabolic effects of temperature, or is related to more favourable environmental conditions remains unclear (Soeffker et al., 2022). However, similar to our findings, there is evidence of a negative influence of warmer temperature on growth, with a negative association between increasing seafloor temperature and both the mean weight and proportion of mature Antarctic toothfish observed across East Antarctica (Yates et al., 2019). Quantifying the influence of temperature on length-at-age and maturity in Antarctic toothfish, therefore, would likely aid our understanding of the vulnerability of these stocks to climate change.

## 5 | CONCLUSION

Our study offers two important conclusions which have direct implications for the stock assessment of Patagonian toothfish in Subarea 48.3. Firstly, given the difficulties inherent in gonadal staging, having an objective method to assess whether an individual Patagonian toothfish is sexually mature based on its length, sex and age, could support expert-determined maturity staging. With careful calibration and testing, such a tool could be phased into the Patagonian toothfish stock assessment alongside or in place of maturity staging from gonads, particularly if temperature experiences can be derived and are deemed important, as suggested by this study and others (e.g., Cheung et al., 2013). Indeed, we advocate for wider consideration of temperature experience in the assessment of length (or age) at maturity for other species (e.g., plaice; Scott & Heikkonen, 2012) and methods (e.g., biphasic growth models; Honsey et al., 2017).

Secondly, the clear negative impact of temperature experienced on Patagonian toothfish length-at-age has implications for this species' stock assessment and management under climate change scenarios. A reduction in length-at-age driven by warmer temperatures could lead to increased juvenile mortality and a reduction in spawning stock biomass with knock-on effects for recruitment. These factors should be considered in future stock assessments of Patagonian toothfish in Subarea 48.3.

## AUTHOR CONTRIBUTIONS

J.E.M. and M.S. conceived the study. S.R.A., S.D.G. and J.E.M. performed the data analysis. P.R.H. processed otolith samples. All authors drafted the manuscript and approved the final version.

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Members for permission to use the data under CCAMLR Data Request 747. Otolith collection and analyses were funded by the Government of South Georgia and the South Sandwich Islands. We also thank Tim Earl for helpful comments on a draft of this manuscript. This manuscript contains public sector information licensed under the Open Government licence v3.

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## DATA AVAILABILITY STATEMENT

Data were obtained from CCAMLR under data request 747 and are not available for public release. Code to simulate from and fit the models is available at https://github.com/CefasRepRes/alewijnse-top-length-at-maturity.

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## REFERENCES

Agnew, D., & Kirkwood, G. P. (2005). A statistical method for estimating the level of IUU fishing: Application to CCAMLR Subarea 48.3. *CCAMLR Science*, *12*, 119–141.

Alewijnse, S. R., & Earl, T. (2025). *Sex-disaggregated biological parameters for Patagonian toothfish (Dissostichus eleginoides) in Subarea 48.3*. CCAMLR. CCAMLR Working Group on WG-SAM-25/26. 18 p.

Amthauer, R., Cárdenas, F., Reyes, A., Valenzuela, A., Dantagnan, P., Vidal, R., & Vargas-Chacoff, L. (2021). Vitellogenesis in the Patagonian toothfish (*Dissostichus eleginoides*) conditioned to a recirculating aquaculture system. *General and Comparative Endocrinology*, *307*, 113768.

Arkhipkin, A. I., Brickle, P., Lee, B., Shaw, P. W., & McKeown, N. J. (2022). Taxonomic re-appraisal for toothfish (*Dissostichus*: Notothenioidea) across the Antarctic Polar Front using genomic and morphological studies. *Journal of Fish Biology*, *100*(5), 1158–1170. https://doi.org/10.1111/jfb.15013

Atkinson, A., Hill, S. L., Pakhomov, E. A., Siegel, V., Reiss, C. S., Loeb, V. J., Steinberg, D. K., Schmidt, K., Tarling, G. A., Gerrish, L., & Sailley, S. F. (2019). Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nature Climate Change*, *9*(2), 142–147. https://doi.org/10.1038/s41558-018-0370-z

Bailey, K. M., & Duffy-Anderson, J. T. (2009). Fish predation and mortality. In J. H. Steele, S. A. Thorpe, & K. K. Turekian (Eds.), *Elements of physical oceanography: A derivative of the encyclopedia of ocean sciences* (pp. 322–329). Elsevier Ltd.

Bamford, C. C. G., Hollyman, P. R., Abreu, J., Darby, C., & Collins, M. A. (2024). Spatial, temporal, and demographic variability in Patagonian toothfish (*Dissostichus eleginoides*) spawning from twenty-five years of fishery data at South Georgia. *Deep Sea Research Part I: Oceanographic Research Papers*, *203*, 104199. https://doi.org/10.1016/j.dsr.2023.104199

Belchier, M., & Collins, M. A. (2008). Recruitment and body size in relation to temperature in juvenile Patagonian toothfish (*Dissostichus eleginoides*) at South Georgia. *Marine Biology*, *155*(5), 493–503. https://doi.org/10.1007/s00227-008-1047-3

Belchier, M., Featherstone, L., & Oliver, J. (2015). *Configuration of the FP-120 net used on UK groundfish surveys in CCAMLR subarea 48.3 (South Georgia)*. CCAMLR. CCAMLR Working Group on Fish Stock Assessment WG-FSA-15/26. 6 p.

Bergmann, C. (1848). *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse*. Vandenhoeck und Ruprecht.

Beverton, R. J., & Holt, S. J. (1957). *On the dynamics of exploited fish populations: Vol. XIX*. Her Majesty's Stationary Office.

Boucher, E. M. (2018). Disentangling reproductive biology of the Patagonian toothfish *Dissostichus eleginoides*: Skipped vs obligatory annual spawning, foraging migration vs residential life style. *Environmental Biology of Fishes*, *101*, 1343–1356. https://doi.org/10.1007/s10641-018-0781-8

Canales-Aguirre, C. B., Ferrada-Fuentes, S., Galleguillos, R., Oyarzun, F. X., & Hernández, C. E. (2018). Population genetic structure of Patagonian toothfish (*Dissostichus eleginoides*) in the Southeast Pacific and Southwest Atlantic Ocean. *PeerJ*, *6*, e4173. https://doi.org/10.7717/peerj.4173

CCAMLR Secretariat. (2025). *Stock Annex 2024: Dissostichus eleginoides at Heard Island (Division 58.5.2)*. https://fishdocs.ccamlr.org/SAannex_HIMI_TOP_2024.pdf

CCAMLR SISO. (2025). *Scheme of international scientific observation scientific observer's manual finfish fisheries*. www.ccamlr.org/node/73033

Cheung, W. W. L., Sarmiento, J. L., Dunne, J., Frölicher, T. L., Lam, V. W. Y., Deng Palomares, M. L., Watson, R., & Pauly, D. (2013). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, *3*(3), 254–258. https://doi.org/10.1038/nclimate1691

CMEMS. (2025). Global ocean physics reanalysis E.U. Copernicus Marine Service Information (CMEMS). Marine Data Store (MDS) [dataset]. https://doi.org/10.48670/moi-00021

Collins, M. A., Brickle, P., Brown, J., & Belchier, M. (2010). Chapter 4 – The Patagonian toothfish: Biology, ecology and fishery. In M. Lesser (Ed.), *Advances in marine biology* (Vol. 58, pp. 227–300). Academic Press. https://doi.org/10.1016/B978-0-12-381015-1.00004-6

Collins, M. A., Hollyman, P. R., Clark, J., Soeffker, M., Yates, O., & Phillips, R. A. (2021). Mitigating the impact of longline fisheries on seabirds: Lessons learned from the South Georgia Patagonian toothfish fishery (CCAMLR Subarea 48.3). *Marine Policy*, *131*, 104618. https://doi.org/10.1016/j.marpol.2021.104618

Collins, M. A., Ross, K. A., Belchier, M., & Reid, K. (2007). Distribution and diet of juvenile Patagonian toothfish on the South Georgia and Shag Rocks shelves (Southern Ocean). *Marine Biology*, *152*(1), 135–147. https://doi.org/10.1007/s00227-007-0667-3

Doonan, I., Large, K., Dunn, A., Rasmussen, S., Marsh, C., & Mormede, S. (2016). Casal2: New Zealand's integrated population modelling tool. *Fisheries Research*, *183*, 498–505. https://doi.org/10.1016/j.fishres.2016.04.024

Earl, T., & Readdy, L. (2023). *Assessment of Patagonian toothfish (Dissostichus eleginoides) in Subarea 48.3*. No. WG-FSA-2023/15 Rev. 1; Report of the CCAMLR Working Group on Fish Stock Assessment. CCAMLR.

Earl, T., Readdy, L., & Marsh, J. (2023). Stock Annex for the 2023 assessment of Subarea 48.3 Patagonian toothfish (*Dissostichus eleginoides*). https://fishdocs.ccamlr.org/SAannex_483_TOP_2024.pdf

Encina-Montoya, F., Vega-Aguayo, R., Oberti-Grassau, C., Mardones-Lazcano, A., Muñoz, G., Barrios-Figueroa, R., Alvarado-Flores, C., Reyes-Campos, A., & Urbina-Foneron, M. A. (2024). First report of Patagonian toothfish (*Dissostichus eleginoides*) metabolic rate and its scaling on a surface culture system. *Brazilian Journal of Biology*, *84*, e285669.

Everson, I., & Murray, A. (1999). Size at sexual maturity of Patagonian toothfish. *CCAMLR Science*, *6*, 37–46.

Farrell, A. P. (2016). Pragmatic perspective on aerobic scope: Peaking, plummeting, pejus and apportioning. *Journal of Fish Biology*, *88*(1), 322–343. https://doi.org/10.1111/jfb.12789

10958649, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.70487 by British Antarctic Survey, Wiley Online Library on [19/05/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Gasco, N., Brown, J., Parker, S., & Duhamel, G. (2011). *Gonad stages identification Dissostichus eleginoides*. WG-FSA-11/39 Rev. 1. Muséum national d'histoire naturelle.

Hanchet, S., Dunn, A., Parker, S., Horn, P., Stevens, D., & Mormede, S. (2015). The Antarctic toothfish (*Dissostichus mawsoni*): Biology, ecology, and life history in the Ross Sea region. *Hydrobiologia*, *761*(1), 397–414. https://doi.org/10.1007/s10750-015-2435-6

Hixon, M. A., Johnson, D. W., & Sogard, S. M. (2014). BOFFFFs: On the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*, *71*(8), 2171–2185. https://doi.org/10.1093/icesjms/fst200

Honsey, A. E., Staples, D. F., & Venturelli, P. A. (2017). Accurate estimates of age at maturity from the growth trajectories of fishes and other ectotherms. *Ecological Applications*, *27*(1), 182–192. https://doi.org/10.1002/eap.1421

Horn, P. L. (2002). Age and growth of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D. mawsoni*) in waters from the New Zealand subantarctic to the Ross Sea, Antarctica. *Fisheries Research*, *56*, 275–287. https://doi.org/10.1016/S0165-7836(01)00325-3

Kock, K.-H., & Kellermann, A. (1991). Reproduction in Antarctic notothenioid fish. *Antarctic Science*, *3*(2), 125–150. https://doi.org/10.1017/S0954102091000172

Marsh, J., Earl, T., Hollyman, P. R., & Darby, C. (2022). *Maturity and growth estimates of Patagonian toothfish in Subarea 48.3 between 2009 to 2021*. CCAMLR. No. WG-FSA-2022/59; Report of the CCAMLR Working Group on Fish Stock Assessment.

Marsh, J. E., Cove, R. J., Britton, J. R., Wellard, R. G., Basic, T., & Gregory, S. D. (2022). Density dependence and environmental variability have stage-specific influences on European Grayling growth. *Oecologia*, *199*, 103–117. https://doi.org/10.1007/s00442-022-05163-2

Massiot-Granier, F., Ouzoulais, F., & Péron, C. (2023a). Stock Annex for the 2023 assessment of the Patagonian toothfish (*Dissostichus eleginoides*) population of the Kerguelen Island EEZ in Division 58.5.1. https://fishdocs.ccamlr.org/SAannex_KI_TOP_2024.pdf

Massiot-Granier, F., Ouzoulais, F., & Péron, C. (2023b). Stock Annex for the 2023 assessment of the Patagonian toothfish (*Dissostichus eleginoides*) population of the Crozet Islands EEZ in Division 58.6. https://fishdocs.ccamlr.org/SAannex_CI_TOP_2024.pdf

Murphy, E. J., Watkins, J. L., Trathan, P. N., Reid, K., Meredith, M. P., Thorpe, S. E., Johnston, N. M., Clarke, A., Tarling, G. A., Collins, M. A., Forcada, J., Shreeve, R. S., Atkinson, A., Korb, R., Whitehouse, M. J., Ward, P., Rodhouse, P. G., Enderlein, P., Hirst, A. G., … Fleming, A. H. (2006). Spatial and temporal operation of the Scotia Sea ecosystem: A review of large-scale links in a krill centred food web. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *362*(1477), 113–148. https://doi.org/10.1098/rstb.2006.1957

Pauly, D. (2019). Female fish grow bigger – let's deal with it. *Trends in Ecology & Evolution*, *34*, 181–182. https://doi.org/10.1016/j.tree.2018.12.007

Plummer, M. (2023). *JAGS: Just another gibbs sampler* (version 4.3.2) [computer software]. https://mcmc-jags.sourceforge.io/

Quinn, T. J., II, & Deriso, R. B. (1999). *Quantitative fish dynamics*. Oxford University Press.

R Core Team. (2024). *R: A language and environment for statistical computing*. Version 4.4.1 [computer software]. R Foundation for Statistical Computing.

Rogers, A. D., Morley, S., Fitzcharles, E., Jarvis, K., & Belchier, M. (2006). Genetic structure of Patagonian toothfish (*Dissostichus eleginoides*) populations on the Patagonian Shelf and Atlantic and western Indian Ocean Sectors of the Southern Ocean. *Marine Biology*, *149*(4), 915–924. https://doi.org/10.1007/s00227-006-0256-x

Saunders, R. A., & Tarling, G. A. (2018). Southern Ocean mesopelagic fish comply with Bermann's rule. *The American Naturalist*, *191*, 343–351. https://doi.org/10.1086/695767

Schulte, P. M. (2015). The effects of temperature on aerobic metabolism: Towards a mechanistic understanding of the responses of ectotherms to a changing environment. *Journal of Experimental Biology*, *218*(12), 1856–1866.

Scott, R., & Heikkonen, J. (2012). Estimating age at first maturity in fish from change-points in growth rate. *Marine Ecology Progress Series*, *450*, 147–157. https://doi.org/10.3354/meps09565

Shaw, P. W., Arkhipkin, A. I., & Al-Khairulla, H. (2004). Genetic structuring of Patagonian toothfish populations in the Southwest Atlantic Ocean: The effect of the Antarctic Polar Front and deep-water troughs as barriers to genetic exchange. *Molecular Ecology*, *13*(11), 3293–3303.

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, *1*(8), 401–406. https://doi.org/10.1038/nclimate1259

Skeljo, F. (2025). *Stock assessment of Patagonian toothfish (Dissostichus eleginoides) in the Falkland Islands to 2024*. Fisheries Report SA-2024-TOO. Fisheries Department, Directorate of Natural Resources, Falkland Islands Government, Stanley, Falkland Islands.

Soeffker, M., Hollyman, P. R., Collins, M. A., Hogg, O. T., Riley, A., Laptikhovsky, V., Earl, T., Roberts, J., MacLeod, E., Belchier, M., & Darby, C. (2022). Contrasting life-history traits of two toothfish (*Dissostichus* spp.) species at their range edge around the South Sandwich Islands. *Deep Sea Research Part II: Topical Studies in Oceanography*, *201*, 105098. https://doi.org/10.1016/j.dsr2.2022.105098

Su, Y. S., & Yajima, M. (2024). *R2jags: Using R to run "JAGS"* (version 0.8-9) [computer software]. https://CRAN.R-project.org/package=R2jags

Thanassekos, S., Reid, K., & Robinson, L. (2025). *CCAMLRGIS: Antarctic spatial data manipulation* [computer software]. https://doi.org/10.32614/CRAN.package.CCAMLRGIS

Thresher, R. E., Koslow, J. A., Morison, A. K., & Smith, D. C. (2007). Depth-mediated reversal of the effects of climate change on long-term growth rates of exploited marine fish. *Proceedings of the National Academy of Sciences*, *104*(18), 7461–7465. https://doi.org/10.1073/pnas.0610546104

Toomey, L., Welsford, D., Appleyard, S. A., Polanowski, A., Faux, C., Deagle, B. E., Belchier, M., Marthick, J., & Jarman, S. (2016). Genetic structure of Patagonian toothfish populations from otolith DNA. *Antarctic Science*, *28*(5), 347–360. https://doi.org/10.1017/S0954102016000183

Trehin, C., Rivot, E., Lamireau, L., Meslier, L., Besnard, A.-L., Gregory, S. D., & Nevoux, M. (2021). Growth during the first summer at sea modulates sex-specific maturation schedule in Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*, 659–669. https://doi.org/10.1139/cjfas-2020-0236

Turner, J., Barrand, N. E., Bracegirdle, T. J., Convey, P., Hodgson, D. A., Jarvis, M., Jenkins, A., Marshall, G., Meredith, M. P., Roscoe, H., Shanklin, J., French, J., Goosse, H., Guglielmin, M., Gutt, J., Jacobs, S., Ii, M. C. K., Masson-Delmotte, V., Mayewski, P., … Klepikov, A. (2014). Antarctic climate change and the environment: An update. *Polar Record*, *50*(3), 237–259. https://doi.org/10.1017/S0032247413000296

Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., Bürkner, P.-C., Paananen, T., & Gelman, A. (2024). *loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models* (version 2.8.0.9000) [computer software]. https://mc-stan.org/loo/

von Bertalanffy, L. (1957). Quantitative laws in metabolism and growth. *The Quarterly Review of Biology*, *32*(3), 217–231. https://doi.org/10.1086/401873

Welsford, D. C., Candy, S. G., Lamb, T. D., Nowara, G. B., Constable, A. J., & Williams, R. (2011). Habitat use by Patagonian toothfish (*Dissostichus eleginoides* Smitt, 1898) on the Kerguelen Plateau around Heard Island and the McDonald Islands. *Cybium*, *35*(SP), 125–136. https://doi.org/10.26028/cybium/2011-35SP-013

Whitehouse, M. J., Meredith, M. P., Rothery, P., Atkinson, A., Ward, P., & Korb, R. E. (2008). Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: Forcings, characteristics and implications for lower trophic levels. *Deep Sea Research Part I: Oceanographic Research Papers*, *55*(10), 1218–1228. https://doi.org/10.1016/j.dsr.2008.06.002

10958649, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.70487 by British Antarctic Survey, Wiley Online Library on [19/05/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Yates, P., Ziegler, P., Welsford, D., McIvor, J., Farmer, B., & Woodcock, E. (2018). Spatio-temporal dynamics in maturation and spawning of Patagonian toothfish *Dissostichus eleginoides* on the sub-Antarctic Kerguelen Plateau. *Journal of Fish Biology*, *92*(1), 34–54. https://doi.org/10.1111/jfb.13479

Yates, P., Ziegler, P., Welsford, D., Wotherspoon, S., Burch, P., & Maschette, D. (2019). Distribution of Antarctic toothfish *Dissostichus mawsoni* along East Antarctica: Environmental drivers and management implications. *Fisheries Research*, *219*, 105338. https://doi.org/10.1016/j.fishres.2019.105338

Zamora-Camacho, F. J., Reguera, S., & Moreno-Rueda, G. (2014). Bergmann's rule rules body size in an ectotherm: Heat conservation in a lizard along a 2200-metre elevational gradient. *Journal of Evolutionary Biology*, *27*(12), 2820–2828. https://doi.org/10.1111/jeb.12546

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