



Original Article

Interactions between ageing error and selectivity in statistical catch-at-age models: simulations and implications for assessment of the Chilean Patagonian toothfish fishery

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In age-structured fisheries stock assessments, ageing errors within age composition data can lead to biased mortality rate and year-class strength estimates. These errors may be further compounded where fishery-dependent age composition data are influenced by temporal changes in fishery selectivity and selectivity misspecification. In this study, we investigated how ageing error within age composition data interacts with time-varying fishery selectivity and selectivity misspecification to affect estimates derived from a statistical catch-at-age (SCA) model that used fishery-dependent data. We tested three key model parameters: average unfished recruitment (R_0), spawning stock depletion (D_{final}), and fishing mortality in the terminal year (F_{terminal}). The Patagonian toothfish (*Dissostichus eleginoides*) fishery in southern Chile was used as a case study. Age composition data used to assess this fishery were split into two sets based on scale (1989–2006) and otolith (2007–2012) readings, where the scale readings show clear age-truncation effects. We used a simulation-estimation approach to examine the bias and precision of parameter estimates under various combinations of ageing error, selectivity type (asymptotic or dome-shaped), selectivity misspecification, and variation in selectivity over time. Generally, ageing error led to overly optimistic perceptions of current fishery status relative to historical reference points. Ageing error generated imprecise and positively biased estimates of R_0 (range 10 to >200%), D_{final} (range –20 to >100%), and F_{terminal} (range –15 to >150%). The bias in D_{final} and R_0 was more severe when selectivity was dome-shaped. Time-varying selectivity (both asymptotic and dome-shaped) increased the bias in D_{final} and F_{terminal} , but decreased the bias in R_0 . The effect of ageing error was more severe, or was masked, with selectivity misspecification. Correcting the ageing error inside the SCA reduced bias and improved precision of estimated parameters.

Keywords: ageing errors, selectivity misspecification, simulation-estimation approach, statistical catch-at-age model, stock assessment, time-varying selectivity.

Introduction

The age-dependent processes of growth, mortality, and reproduction are critical in fisheries science, extending everywhere from the general theory of fishing, to specific harvest advice derived from fisheries stock assessments (Tyler *et al.*, 1989; Bradford, 1991). For example, in statistical catch-at-age (SCA) analysis, age

information (from surveys or fisheries) is used to model maturity and growth schedules, natural mortality rates, and year-to-year variation in recruitment to fish populations (Maunder and Punt, 2013). Ageing errors, such as underestimation of age, can affect the accuracy (i.e. the closeness of the age estimate to the “true” value) and precision (i.e. the agreement or variability between

readings of the same specimen by the same or different age-readers) of age information (Kimura and Lyons, 1991). Unfortunately, systematic underestimation of age remains a problem for many fish stocks because obtaining accurate and precise age estimates is expensive and time-consuming (Cardinale and Arrhenius, 2004; Begg *et al.*, 2005). Generally, even the more reliable ageing methods, such as bomb radiocarbon analysis, can be subject to bias and imprecision that alters the stock assessment results (e.g. Stewart and Piner, 2007).

Fish ages determined via low-resolution methods, such as scales or whole-otoliths, may lead to biased estimates of the population age structure and, therefore, erroneous stock assessment estimates of spawning biomass, recruitment, and fish population productivity (Mills and Beamish, 1980; Richards *et al.*, 1992; Yule *et al.*, 2008). For example, ageing error affected estimates of spawning-stock biomass and fishing mortality for Atlantic cod (*Gadus morhua*) in the Eastern Baltic, leading to overly optimistic total allowable catch (TAC) and ineffective conservation measures (Reeves, 2003). Similarly, Yule *et al.* (2008) postulated that the collapse of cisco (*Coregonus artedii*) in the Great Lakes was linked, in part, to a systematic underestimation of the fish ages determined from scales. For recruitment in particular, biased age estimates cause strong year-classes to appear weaker and weak year-classes to appear stronger (Fournier and Archibald, 1982; Kimura and Lyons, 1991; Richards *et al.*, 1992), leading to misinterpretation of the stock–recruit analyses (Bradford, 1991). By degrading our understanding of fish production, ageing errors also reduce the quality of the risk assessments associated with future management strategies (Fournier and Archibald, 1982; Richards *et al.*, 1992; Punt *et al.*, 2008).

Fishery selectivity also plays a critical role in SCA; however, there is generally little research exploring selectivity in fisheries stock assessments (Sampson, 2014), or how selectivity might interact with the other assumptions built into stock assessment models. SCA models can be sensitive to misspecification of selectivity, which can occur when using the incorrect shape (asymptotic vs. dome-shaped) or when incorrectly assuming that selectivity is constant over time (Linton and Bence, 2011). Time-varying selectivity should be expected in fishery-dependent data because selectivity is highly influenced by the fishing gear, characteristics of the fleet, effort levels, spatial distribution of effort, and movement of the fish (Sampson, 2014). Ignoring changes in selectivity over time can lead to biased estimates of uncertainty, management quantities, and biological reference points (Goodyear, 1996; Maunder and Piner, 2015).

Although several studies examine the influence of ageing errors on stock assessments and fisheries advice (Fournier and Archibald, 1982; Rivard, 1989; Restrepo and Powers, 1990; Bradford, 1991; Coggins and Quinn, 1998; Reeves, 2003; Bertignac and de Pontual, 2007; Punt *et al.*, 2008; Dorval *et al.*, 2013; Liao *et al.*, 2013), few studies evaluate how ageing errors and the selectivity assumptions combine to affect stock assessment model reliability. Since both ageing error and the selectivity assumptions can have independent effects on recruitment estimates and perceptions of stock status and fishing mortality, it must be emphasized to consider their interaction. Stock assessment model performance can be improved by accounting for these effects. While it is difficult to measure, and thus correct, the fishing selectivity, a correction can be applied to the age composition data, when the ageing error is known.

In this study, we used a simulation-estimation approach to investigate: (i) how the SCA model parameter estimates are affected by ageing error within the age composition data, selectivity type

(asymptotic or dome-shaped), selectivity variation over time, and selectivity misspecification, and (ii) under what conditions correcting the ageing error inside the SCA model leads to improvements in the stock assessment model performance. The simulation-estimation approach is widely used to evaluate the robustness of estimation models to different assumptions, input data, and misspecification of model components (Linton and Bence, 2008; Wetzel and Punt, 2011; Deroba and Schueller, 2013). In this approach, an operating model (OM) simulates the population and fishery dynamics from true parameter values that are known exactly (Smith, 1993; Butterworth and Punt, 1999; Wetzel and Punt, 2011). This OM is used to generate data under different stock assessment configurations that is fit by the estimation model (e.g. SCA). This allows comparison of the estimation model output with true dynamics simulated in the OM.

For our simulation-estimation, we developed an OM parameterized using the biological and fishery characteristics of the Chilean Patagonian toothfish (*Dissostichus eleginoides*) fishery (Table 1). The Patagonian toothfish supports one of the most lucrative fisheries operating in the Antarctic and Subantarctic waters off the southern cone of South America between 47°S and the limit of Chile's Exclusive Economic Zone. The Patagonian toothfish is a deep-water species with slow growth, late maturity, and great longevity, often living to >50 years (Horn, 2002; Belchier, 2004). Currently, the Chilean Patagonian toothfish stock is in an overfished and overfishing state (Tascheri and Canales, 2015). Age composition data for the Patagonian toothfish fishery off southern Chile contain ageing errors due to the inconsistent use of scales and otoliths for ageing. Therefore, it is an ideal case study for testing the effects of ageing error and selectivity assumptions in stock assessments.

Age composition for Patagonian toothfish was obtained from scale readings between 1989 and 2006; since then, age composition has been determined from thin transverse sections of otoliths. Significant differences exist between the ages determined from scales and otoliths. For fish aged from scales, overlapping rings on the scale edge led to low resolution in older ages (Tyler *et al.*, 1989), causing old fish to appear younger and underestimating the contribution of older fish to the catch. Switching to otolith readings raised the maximum estimated age from 23 to over 30 years (Ashford *et al.*, 2001). Therefore, biomass estimates and other management quantities have probably been biased by these differences.

Methods

Overview

The general simulation-estimation framework consisted of four main steps: (i) constructing an OM to simulate, over 24 years, the true population and fishery dynamics, including process errors in recruitment and selectivity (if applicable) and observation errors in catchability, age-composition data, and fishery catch-per-unit-effort (cpue), (ii) applying the SCA estimation model to the simulated data, (iii) repeating steps (i) and (ii) 100 times, and (iv) calculating performance statistics for the estimated fishery and management parameters relative to their true values from the OM (Figure 1). Parameters for each OM were obtained by conditioning the model to one of the four cases defined below.

Operating model

Parameter definitions and equations used to describe the OM are presented in Table 1 and Appendix A (Table A1). The OM simulates key aspects of the fish population and fishery dynamics and is used

Table 1. Description and values for abundance index, structural parameters, state variables, derived variables, and stochastic deviation used in the Patagonian toothfish population dynamics, operating, and estimation model.

Symbols	Description	Value	Estimation model
Index variables			
t	Annual time-step $T = 24$ (1989–2012)	$\{1, 2, \dots, T\}$	$\{1, 2, \dots, T\}$
a	Age-class in years where $A = 30$	$\{1, 2, \dots, A\}$	$\{1, 2, \dots, A\}$
Structural parameters			
l_{∞}	Mean asymptotic size (mm) ^a	2871	2871
k	Growth coefficient (year ⁻¹) ^a	0.021	0.021
a_0	Mean length-at-age at zero age (year) ^a	-4.289	-4.289
$c-d$	Scaling constant for weight-at-length (mm to tonnes) ^a – allometric factor ^a	2.59e-12-3.206	2.59e-12-3.206
a_{50}	Age-at-50% maturity ^b	14	14
a_{95}	Age-at-95% maturity ^b	17	17
M	Instantaneous natural mortality (year ⁻¹)	0.15	0.15
F	Average fishing mortality rate		Estimated
h	Steepness h	0.60	0.60
R_0	Unfished recruitment	1 210 070	Estimated
σ_R	Standard deviation for the recruitment deviations	0.6	0.6
q	Catchability coefficient for catch-per-unit-effort (cpue)	0.0154	Estimated
σ_I	Standard deviation for the cpue	0.2	0.2
q_t	Time-varying catchability coefficients for cpue	–	–
σ_q	Standard deviation for the random walk (rw) for time-varying q	0.1	–
ρ_q	Correlation coefficient for the rw for time-varying q	0.9	–
$\Omega_1 - \Omega_2$	Age-at-50% and age-at-95% (time-invariant logistic selectivity)	10–14	Estimated
Ω_3, Ω_4	Inflection 1, inflection 2 (time-invariant double logistic selectivity)	10–8	Estimated (Ω_3)
Ω_5, Ω_6	slope 1, and slope 2 (time-invariant double logistic selectivity)	0.65–0.09	Estimated (Ω_5)
Ω_{1t}	Age-at-50% (time-varying logistic selectivity)		Estimated
$\sigma_{\Omega 1}$	Standard deviation for the rw for age-at-50% (time-varying logistic selectivity)	7	
$\rho_{\Omega 1}$	Correlation coefficient for the rw for age-at-50% (time-varying logistic selectivity)	0.1	–
$L_{\Omega 1}$	Lower bound for the rw for age-at-50% (time-varying logistic selectivity)	5	–
$U_{\Omega 1}$	Upper bound for the rw for age-at-50% (time-varying logistic selectivity)	10	–
$\Omega_{3t} - \Omega_{4t}$	Inflection 1 and inflection 2 (time-varying double logistic selectivity)		Estimated (Ω_{3t})
$\sigma_{\Omega 3} - \sigma_{\Omega 4}$	Standard deviation for the rw for inflection 1 and inflection 2 (time-varying double logistic selectivity)	1	–
$\rho_{\Omega 3} - \rho_{\Omega 4}$	Correlation coefficient for the rw for inflection 1 and inflection 2 (time-varying double logistic selectivity)	0.1	–
$L_{\Omega 3} - L_{\Omega 4}$	Lower bound for the rw for Ω_3 and Ω_4	4	–
$U_{\Omega 4} - U_{\Omega 3}$	Upper bound for the rw for Ω_3 and Ω_4	11	–
σ_5	Standard deviation for the rw for Ω_1 and Ω_3 (SCA model)	–	5–1
State variables			
$N_{a,t}$	Number-at-age a in year t		
$Z_t (M + F_t)$	Instantaneous total mortality		
$C_{a,t}$	Catch-at-age in numbers		
$P_{a,t}$	Observed proportion-at-age		
$\hat{P}_{a,t}$	Predicted proportion-at-age		
SSB_t	Spawning biomass in year t (t)		
C_t	Catch in year t (t)		
VB_t	Exploitable biomass (t)		
$cpue_t$	Catch-per-unit-effort in year t		
Derived variables			
B_0	Unfished spawning biomass (t)		
S_a	Selectivity-at-age		
m_a	Mature proportion-at-age		
l_a	Length-at-age (cm)		
w_a	Body mass-at-age (tonnes)		
ϕ	Unfished equilibrium spawning biomass per recruit (t)		
Stochastic deviation			
w_t	Lognormal random recruitment deviates		Estimated
ε_t	Lognormal random cpue deviates		–
f_t	Lognormal random fishing mortality deviates		Estimated
φ_t	Random q deviates		–

Continued

Table 1. Continued

Symbols	Description	Value	Estimation model
$\delta_t (\Omega_{1t})$	Logistic selectivity deviates for rw		Estimated
$\delta_t (\Omega_{3t})$	Double logistic selectivity deviates for rw		Estimated
Others			
$N_{fishery}$	Sample size for catch-at-age	800	200
SV	Sampling variability	Multinomial	Multinomial

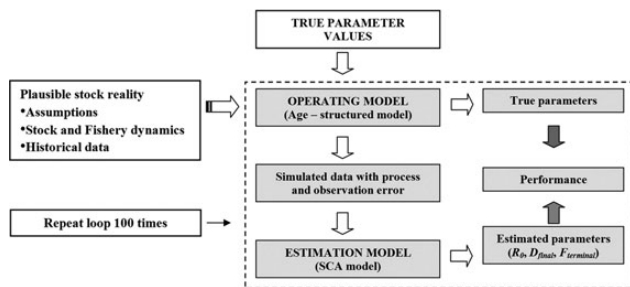
^aZiegler (2013).^bArana (2009).

Figure 1. General conceptual scheme of the simulation-estimation procedure (modified from Wetzel and Punt, 2011).

to generate data, including catches, age composition, and cpue for the SCA. Our base model was a single-sex, age-structured population dynamics model with fish ages 1–30+ years, where 30+ is a group containing all fish aged 30 years and older. An exponential population dynamics model was used to project abundance for each age, with total mortality partitioned into instantaneous fishing mortality and natural mortality [Equation (A3.1)]. Annual recruitment of age-1 fish followed a Beverton–Holt stock–recruitment relationship parameterized in terms of steepness (h), with lognormal random deviates [Equation (A3.2)]. The spawning-stock biomass (SSB_t) at year t was calculated as the sum of the product of number-at-age, proportion mature-at-age, and weight-at-age [Equation (A3.3)]. Numbers-at-age in the first year included lognormal random deviates [Equation (A4.1)].

In the OM, four fishery selectivity cases were defined by combining logistic and double logistic curve with time-invariant and time-varying dynamics (Figure 2). Time-invariant logistic selectivity was modelled as shown in Equation (A5.1). For the time-varying logistic selectivity function, the age-at-50% selectivity (Ω_1) varied year-to-year following an autocorrelated random walk [Equation (A5.2)]. The time-invariant double-logistic function was modelled as presented in Equation (A5.3). The term $\text{MAX}_a(\text{num})_a$ indicates the maximum value of the numerator. This term normalized the age-specific selectivity, so that fully selected individuals had a value of 1.0. For the time-varying double logistic selectivity function, the inflection 1 (Ω_3) and inflection 2 (Ω_4) parameters varied over time following an autocorrelated random walk [Equation (A5.4)]. Details are given in Appendix A (A5).

The catch-at-age in numbers was calculated using the Baranov equation [Equation (A6.1)]. The catch during year t is calculated as the sum of the product of catch-at-age (in numbers) and weight-at-age [Equation (A6.2)]. Age composition was transformed to proportions-at-age using Equations (A6.3–A6.4). Observed catch-at-age data were simulated using random draws, from a multinomial distribution with a sample size of 800 [Equation (A6.5)].

Ageing error in the age composition differed between the scale-based and otolith-based data. The scale readings generated a systematic underestimation of the age (bias), while the otolith readings generated an imprecise estimation. For the first 18 years of the fishery, the observed catch-at-age was derived from scale-based readings and, for the final 6 years, it was derived from otolith-based readings. These ageing errors were introduced by multiplying the observed catch-at-age by two matrices: $P(a'|a)$ and $E(a'|a)$. $P(a'|a)$ is an ageing error probability matrix that mimics the ageing error for scale readings [Equation (A6.6)], while $E(a'|a)$ is an ageing error probability matrix for otolith readings [Equation (A6.7)]. Details of the $P(a'|a)$ and $E(a'|a)$ terms are given in the ageing error procedure section.

Fishery cpue in the OM included observation error as lognormal random deviates corrected for lognormal bias [Equations (A7.1–A7.2)]. The catchability coefficient was a constant parameter (q) or a time-varying random walk (q_t) depending on the cases and scenarios [see the Fishery-dependent information section in Appendix A (A7)].

Ageing error procedure

The ageing error probability matrix $P(a'|a)$ had rows and columns corresponding to scale ages a' and otolith ages a , respectively. This matrix specifies the probability that a fish with age a , from otoliths, was allocated to an age a' , from scales. The probability in the matrix had constraints $P(a'|a) \geq 0$ and $\sum_{a'=1}^A P(a'|a) = 1$ for each a .

We used a sample of 392 fish to model the relationship between scale-based and otolith-based ages. For each fish, the age was estimated from both scales and otoliths. The age reproducibility experiment was carried out by a reader from the Chilean Fisheries Development Institute (IFOP). This reader had experience in reading both scales and otoliths from Patagonian toothfish. Unfortunately, the data did not cover the whole age range. However, we predicted the relationship at older ages from the available information (Figure 3).

The expected scale age (Y), as a function of the observed otolith age (X), followed a logistic model, i.e. $Y = y_{\max}(1 - \exp^{-mX})$, where $y_{\max}$ and m are the maximum predicted scale age and slope, respectively. The probabilities in the matrix $P(a'|a)$ were generated assuming a normal distribution with mean Y and variance $\hat{\sigma}_{sc}^2$; $\hat{\sigma}_{sc}$ is the predicted standard deviation of the mean scale age, given an otolith age. To estimate $\hat{\sigma}_{sc}$, the observed standard deviation of the mean scale age (σ_{sc}) was fit as a function of the otolith age (X). This relationship was a power function; $\hat{\sigma}_{sc} = a_1 \times X^{b_1}$, where a_1 and b_1 are the scale and the shape parameters, respectively. The model was fit using data from ages 5–11. For ages outside of this range, σ_{sc} was predicted from the model.

In addition, we used a Bayesian approach to estimate the parameters $y_{\max}$ and m . Uninformative priors were used for $y_{\max}$ and

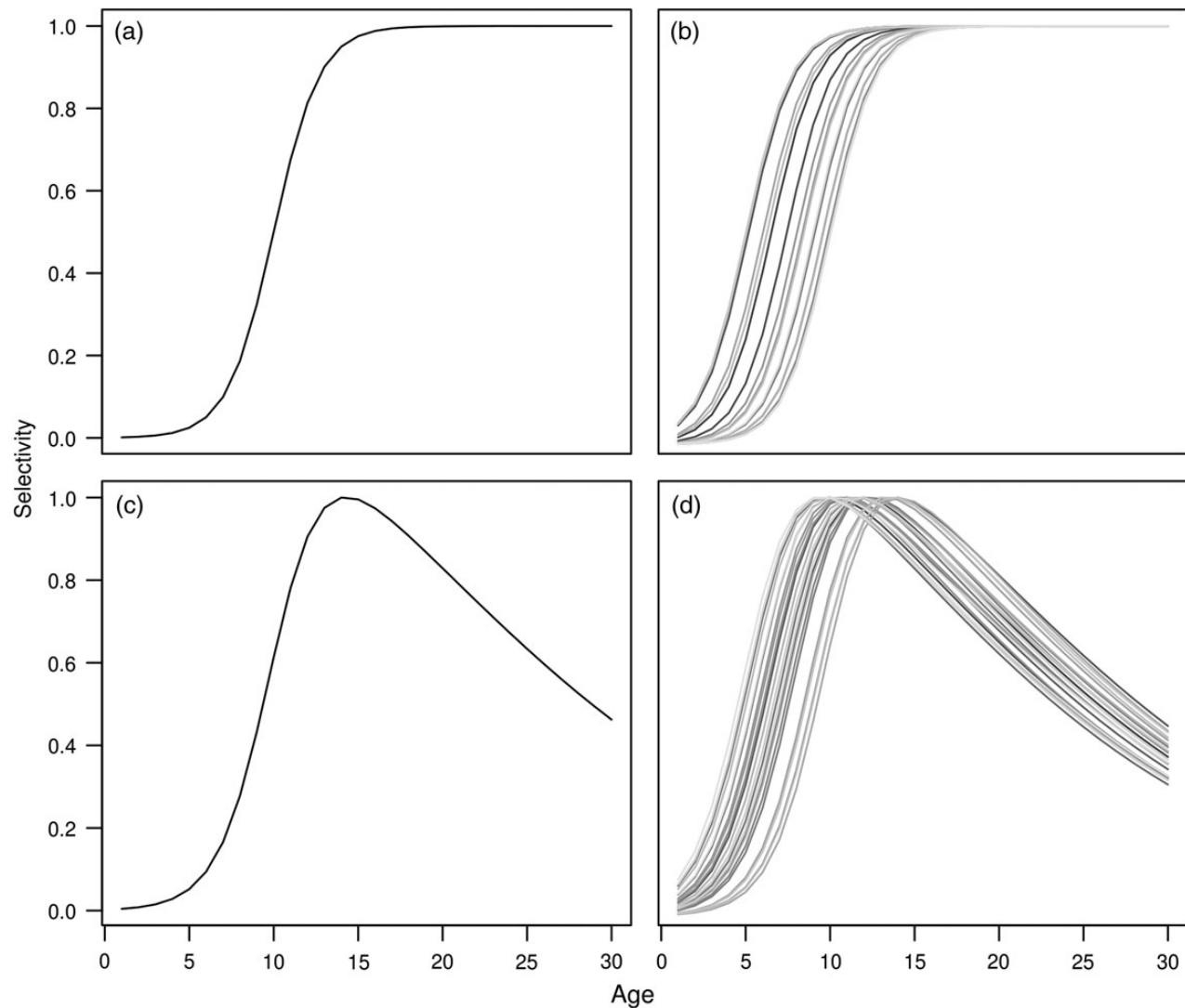


Figure 2. Selectivity curves of one random simulation used by the OM to generate data. (a) Logistic selectivity, (b) time-varying logistic selectivity, (c) double logistic selectivity, and (d) time-varying double logistic selectivity.

m and the Metropolis–Hastings algorithm in the R package MCMCpack (Martin *et al.*, 2011) was used to approximate the posterior distribution. For the simulation-estimation experiments, we sampled 100 ($y_{\max}$, m) pairs from the joint posterior distribution to obtain a different $P(a'|a)$ for each simulation. An example age-reading error matrix can be found in the Supplementary Table S1.

The ageing error probability matrix $E(a'|a)$, was modelled following the same procedure used in $P(a'|a)$. However, the matrix $E(a'|a)$ has rows and columns corresponding to otolith ages a' read by the reader 2 and otolith ages a read by the reader 1, respectively.

A study by Welsford *et al.* (2012), using otoliths from Patagonian toothfish, showed a linear relationship between different readers. We used the slope (m_2) and intercept (I) reported in this study to model the relationship between the expected mean otolith age estimated by reader 2 (X_2), as a function of the age estimated by reader 1 (X_1); $X_2 = I + m_2 X_1$.

The probabilities in the matrix $E(a'|a)$ were generated assuming a normal distribution, with mean X_2 and variance σ_{ot}^2 . σ_{ot} is the

predicted standard deviation of the mean otolith age estimated by reader 2, given the otolith age estimated by reader 1 and was set to 0.15 for all the ages. Thus, unlike the $P(a'|a)$ matrix, the $E(a'|a)$ matrix includes imprecision in the ageing process but not bias.

The OM was implemented in the statistical software R (R Core Team, 2014). Full details for the population dynamics model and equations can be found in Appendix A.

Estimation model

The estimation procedure was performed using an SCA model. The estimation model basically follows the same population dynamics equations as the OM to generate the datasets. However, in the SCA, some of the OM parameters were estimated, while other parameters, such as natural mortality, steepness, growth, and maturity parameters, and standard deviation of the stock–recruit relationship, were fixed at their true values. The parameters estimated in the SCA included the yearly fishing mortalities, the fishery selectivity parameters, the average unfished recruitment (R_0), and a time-series of deviations around average recruitment. Under some scenarios,

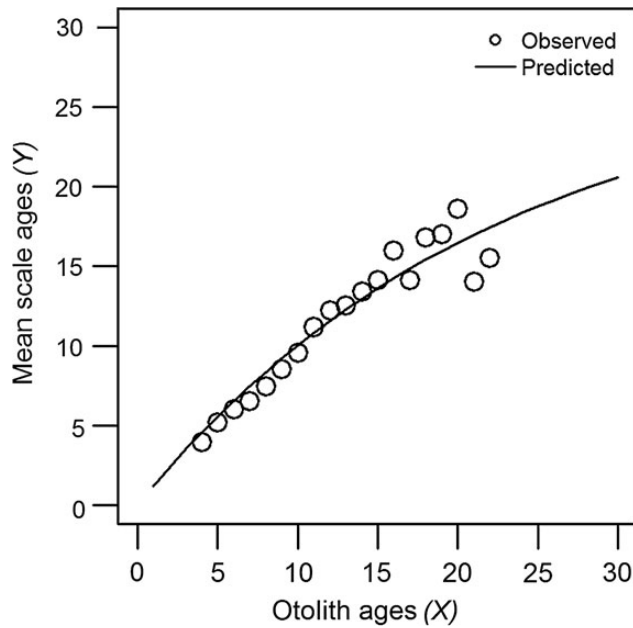


Figure 3. Relationship between scale-based and otolith-based ages from individual fish. Each point represents the mean ages observed in scales corresponding to each otolith age. The line represents the predicted ages obtained after fitting the logistic model.

the selectivity was time-varying; this increased the number of parameters that were estimated. Depending on the scenario, these parameters included the age-at-50% selectivity (Ω_1) in the logistic function, the first (Ω_3) inflection and first slope (Ω_5) points of the double-logistic function, and the annual deviations for Ω_1 and Ω_3 . In the SCA, the catchability parameter (q) was only estimated as a time-invariant parameter, but depending on the scenario, was time-invariant or time-varying in the OM (Table 1).

The parameters were estimated using a penalized maximum likelihood procedure implemented in AD Model Builder (Fournier *et al.*, 2012). The objective function included likelihood components for the cpue, catches, and age compositions of the fishery (Appendix B; Table B1). The SCA model assumed lognormal distribution errors for catches [Equation (B1.2)] and fishery cpue [Equation (B1.3)], and a multinomial distribution for the age composition [Equation (B1.4)], with an effective sample size of 200. The minimization of the objective function was performed in phases. In the initial phase, the estimates of the expected average fishing mortality were penalized; this constraint was removed during the final phase of fitting. We assumed that the model had converged if the maximum gradient was less than 0.0001. The model notation and parameters are given in Table 1. Details of the SCA model can be found in Appendix B.

Ageing error correction procedure

To correct the ageing errors obtained from scale readings, the maximum likelihood estimates of $y_{\max}$ and m were used to generate the $P_{\text{MLE}}(a'|a)$. We multiplied the predicted age-proportion for the years 1989 to 2006 (from the SCA) [Equation (B2.1)] by the transpose of the $P_{\text{MLE}}(a'|a)$ matrix to obtain a predicted scale-based age composition. This “corrected” age composition matrix was then input into the multinomial likelihood. Details of the ageing error correction procedure are in Appendix B (B2).

Simulation cases

Four general simulation-estimation cases with time-varying or time-invariant selectivity were created to explore the SCA performance (Table 2). In each case, selectivity in the OM and the SCA were identical, except that the true parameters were unknown in the SCA. The selectivity functions were time-invariant logistic (TI-L), time-invariant double logistic (TI-DL), time-varying logistic (TV-L), and time-varying double logistic (TV-DL). For each of these selectivity cases, we generated data from the OM under three scenarios that combine ageing error with constant catchability: (i) no ageing error with constant catchability (NAE-1), (ii) ageing error with constant catchability (AE-1), and (iii) ageing error with an age-correction matrix and constant catchability (AEC-1). Similarly, we generated data from the OM under three scenarios with time-varying catchability. The time-varying catchability scenarios are labelled similarly to the scenarios with constant catchability, except a “2” is used in place of “1”. A description of the four cases and six scenarios is given in Table 2.

Additionally, we explored SCA performance under another four cases with selectivity misspecification. In each case, selectivity differed between the OM and the SCA. The case configurations were: (i) time-invariant logistic selectivity in the OM and time-invariant double logistic selectivity in the SCA (TI-L_TI-DL); (ii) time-invariant double logistic selectivity in the OM and time-invariant logistic selectivity in the SCA (TI-DL_TI-L); (iii) time-varying logistic selectivity in the OM and time-invariant logistic selectivity in the SCA (TV-L_TI-L); and (iv) time-varying double logistic selectivity in the OM and time-invariant double logistic selectivity in the SCA (TV-DL_TI-DL). For each of these cases, the data were generated from the OM under the following four scenarios that combine ageing error with and without time-varying catchability: (i) no ageing error with constant catchability (NAE-1), (ii) no ageing error with time-varying catchability (NAE-2), (iii) ageing error with constant catchability (AE-1), and (iv) ageing error with time-varying catchability (AE-2). A description of these four cases and four scenarios is given in Tables 3 and 4.

Performance statistics

Estimation performance for the SCA was evaluated against the true OM values for all of the scenarios in each of the cases. Performance measures were computed for the parameters R_0 , D_{final} , and F_{terminal} because these are most closely related to management reference points. R_0 is the unexploited recruitment level before starting the fishery. D_{final} is the spawning biomass depletion, or the ratio between the spawning biomass, from a given year, and the unexploited spawning biomass. F_{terminal} is the fishing mortality rate in the most recent year. The bias (i.e. the error that affects the closeness of the parameter estimate to the true value) and precision (i.e. the degree of reproducibility between repeated estimates) of the parameter estimates were assessed. The bias and precision of the SCA were determined by calculating the median relative error (RE) and the median absolute relative error (MARE) for R_0 , D_{final} , and F_{terminal} for each trial, relative to the OM values. This resulted in 100 RE and MARE values for each case–scenario combination. The RE and MARE were calculated as:

$$RE_{i,j} = 100 \times \frac{E_{i,j} - T_{i,j}}{T_{i,j}}, \quad (1)$$

$$\text{MARE}_{i,j} = 100 \times \left(\left| \frac{E_{i,j} - T_{i,j}}{T_{i,j}} \right| \right), \quad (2)$$

Table 2. OM characteristics for each case used in the estimation model and the median absolute relative error (MARE) values of D_{final} , R_0 , and F_{terminal} obtained for the four cases.

Case	Scenario	Selectivity (OM – EM)	Catchability (OM) ^a	Ageing error in OM	Ageing error correction in EM	MARE (%)		
						D_{final}	R_0	F_{terminal}
TI-L	NAE-1 ^b	Time-invariant logistic	Time-invariant	No	–	8.583	14.567	22.572
	AE-1 ^c	Time-invariant logistic	Time-invariant	Yes	No	21.998	95.917	50.414
	AEC-1	Time-invariant logistic	Time-invariant	Yes	Yes	11.774	19.287	14.957
	NAE-2	Time-invariant logistic	Time-varying	No	–	9.837	21.647	17.567
	AE-2	Time-invariant logistic	Time-varying	Yes	No	26.434	106.154	38.803
	AEC-2	Time-invariant logistic	Time-varying	Yes	Yes	11.302	21.485	14.179
TI-DL	NAE-1	Time-invariant double logistic	Time-invariant	No	–	9.339	15.344	18.587
	AE-1	Time-invariant double logistic	Time-invariant	Yes	No	35.973	112.214	41.196
	AEC-1	Time-invariant double logistic	Time-invariant	Yes	Yes	14.151	15.340	14.787
	NAE-2	Time-invariant double logistic	Time-varying	No	–	12.547	18.782	15.664
	AE-2	Time-invariant double logistic	Time-varying	Yes	No	40.755	105.816	34.836
	AEC-2	Time-invariant double logistic	Time-varying	Yes	Yes	11.674	17.863	14.582
TV-L	NAE-1	Time-varying logistic	Time-invariant	No	–	13.732	16.692	18.002
	AE-1	Time-varying logistic	Time-invariant	Yes	No	24.603	79.447	61.756
	AEC-1	Time-varying logistic	Time-invariant	Yes	Yes	12.636	21.084	20.137
	NAE-2	Time-varying logistic	Time-varying	No	–	15.046	25.450	18.585
	AE-2	Time-varying logistic	Time-varying	Yes	No	36.037	103.693	45.096
	AEC-2	Time-varying logistic	Time-varying	Yes	Yes	16.302	25.737	19.084
TV-DL	NAE-1	Time-varying double logistic	Time-invariant	No	–	18.512	14.192	13.857
	AE-1	Time-varying double logistic	Time-invariant	Yes	No	55.272	78.829	43.179
	AEC-1	Time-varying double logistic	Time-invariant	Yes	Yes	13.871	17.320	15.651
	NAE-2	Time-varying double logistic	Time-varying	No	–	24.401	19.888	14.209
	AE-2	Time-varying double logistic	Time-varying	Yes	No	53.363	96.567	31.944
	AEC-2	Time-varying double logistic	Time-varying	Yes	Yes	14.775	13.167	16.561

^aCatchability was always estimated as a constant parameter in the EM.^bNAE-1 represent the base scenario.^cAE-1 represent the null scenario, where only the ageing error is considered, under time-invariant logistic selectivity.**Table 3.** OM characteristics for each case used in the estimation model with selectivity misspecification in the absence of ageing error (NAE), and the median absolute relative error (MARE) values of D_{final} , R_0 , and F_{terminal} obtained for the four cases for each selectivity configuration [for comparison, the scenarios where the selectivity was correctly specified, that is, the selectivity function used in the OM was maintained in the SCA, are presented in parentheses (see Table 2 for scenario names)].

		Selectivity		MARE (%)		
Case	Scenario	OM	SCA	D_{final}	R_0	F_{terminal}
Selectivity incorrectly specified in the SCA (without ageing error)						
TI-L_TI-DL	NAE-1	Time-invariant logistic	Time-invariant double logistic	8.960 (8.583)	13.566 (14.567)	15.619 (22.572)
	NAE-2	Time-invariant logistic	Time-invariant double logistic	10.993 (9.837)	13.360 (21.647)	14.759 (17.567)
TI-DL_TI-L	NAE-1	Time-invariant double logistic	Time-invariant logistic	11.038 (9.339)	31.356 (15.344)	26.204 (18.587)
	NAE-2	Time-invariant double logistic	Time-invariant logistic	15.826 (12.547)	41.803 (18.782)	21.951 (15.664)
TV-L_TI-L	NAE-1	Time-varying logistic	Time-invariant logistic	24.074 (13.732)	23.476 (16.692)	39.829 (18.002)
	NAE-2	Time-varying logistic	Time-invariant logistic	27.418 (15.046)	21.224 (25.450)	45.229 (18.585)
TV-DL_TI-DL	NAE-1	Time-varying double logistic	Time-invariant double logistic	23.571 (18.512)	14.543 (14.192)	20.337 (13.857)
	NAE-2	Time-varying double logistic	Time-invariant double logistic	21.122 (24.401)	16.301 (19.888)	21.042 (14.209)

Number 1 in scenarios indicates a time-invariant catchability in the OM, and number 2 in scenarios indicates a time-varying catchability in the OM.

where $E_{i,j}$ is the estimated value for parameter i for simulation j , and $T_{i,j}$ is the true value for parameter i for simulation j . Changes in model performance among scenarios were evaluated by comparison of the RE and $MARE$ values.

Results

Figure 4 and Table 2 present the results of the scenarios where the selectivity was correctly specified (i.e. the same function of selectivity was used in the OM and in the SCA model); the data were generated without ageing error, with ageing error, and with an ageing

correction inside the SCA model. The results also show the scenarios where either a time-invariant or time-varying catchability was used in the OM.

Effect of ageing error on parameter estimates and its interaction with time-invariant and time-varying selectivity

The model parameters, D_{final} and R_0 , were estimated with low bias (median RE below 10%) and good precision ($MARE$ below 15%), when there was no ageing error, the selectivity was a logistic

Table 4. OM characteristics for each case used in the estimation model with selectivity misspecification in the presence of ageing error (AE), and the median absolute relative error (MARE) values of D_{final} , R_0 , and F_{terminal} obtained for the four cases for each selectivity configuration (for comparison, the scenarios where the selectivity was correctly specified, that is, the selectivity function used in the OM was maintained in the SCA, are presented in parentheses (see Table 2 for scenario names).

		Selectivity		MARE (%)		
Case	Scenario	OM	SCA	D_{final}	R_0	F_{terminal}
Selectivity incorrectly specified in the SCA (with ageing error)						
TI-L_TI-DL	AE-1	Time-invariant logistic	Time-invariant double logistic	31.547 (21.998)	50.061 (95.917)	40.338 (50.414)
	AE-2	Time-invariant logistic	Time-invariant double logistic	34.792 (26.434)	55.076 (106.154)	30.116 (38.803)
TI-DL_TI-L	AE-1	Time-invariant double logistic	Time-invariant logistic	27.896 (35.973)	213.237 (112.214)	53.073 (41.196)
	AE-2	Time-invariant double logistic	Time-invariant logistic	37.374 (40.755)	215.518 (105.816)	47.734 (34.836)
TV-L_TI-L	AE-1	Time-varying logistic	Time-invariant logistic	30.333 (24.603)	60.904 (79.447)	44.211 (61.756)
	AE-2	Time-varying logistic	Time-invariant logistic	36.853 (36.037)	67.310 (103.693)	35.901 (45.096)
TV-DL_TI-DL	AE-1	Time-varying double logistic	Time-invariant double logistic	32.610 (55.272)	70.380 (78.829)	31.934 (43.179)
	AE-2	Time-varying double logistic	Time-invariant double logistic	36.150 (53.363)	94.847 (96.567)	24.944 (31.944)

Number 1 in scenarios indicates a time-invariant catchability in the OM, and number 2 in scenarios indicates a time-varying catchability in the OM.

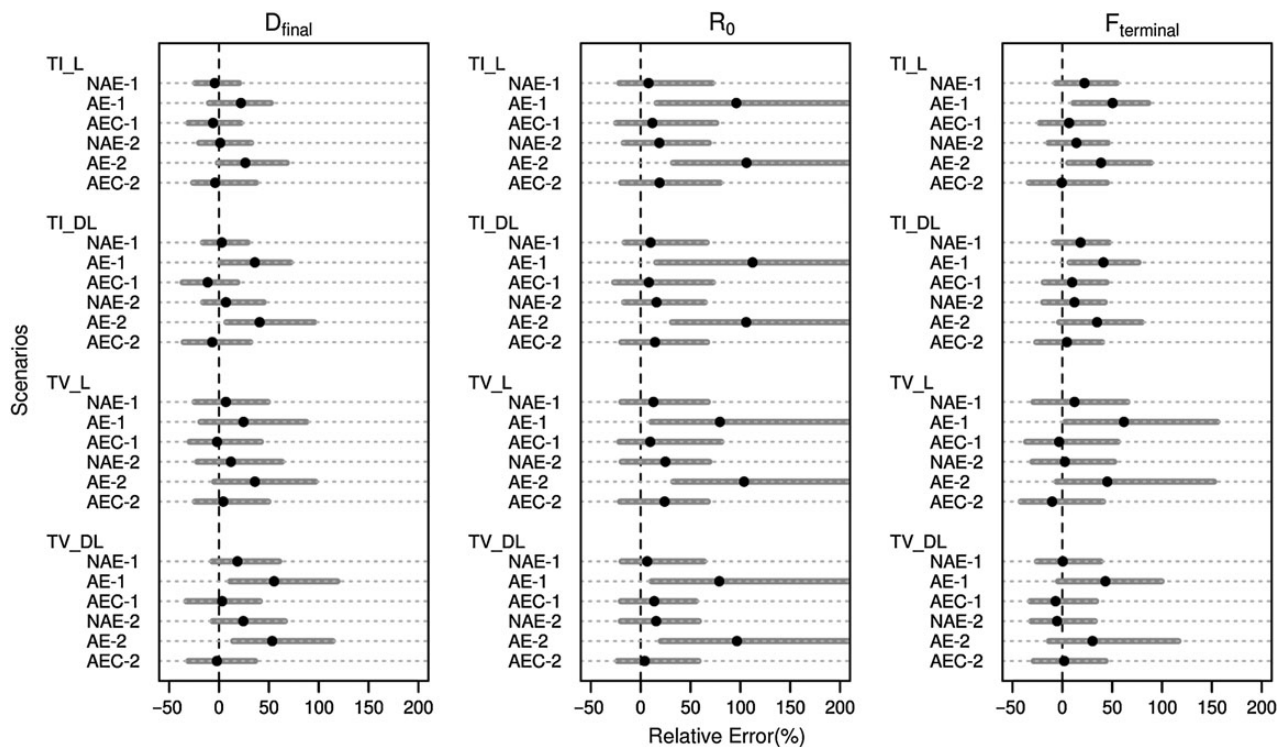


Figure 4. Median relative errors (black dots) and the central 90% confidence interval (grey line), for D_{final} , R_0 , and F_{terminal} , for the four cases – six scenario combinations. Time-invariant logistic (TI-L), time-invariant double logistic (TI-DL), time-varying logistic (TV-L), and time-varying double-logistic (TV-DL). The cases and scenarios descriptions are given in Table 2.

function, and catchability was a constant parameter in both the OM and the SCA (base scenario TL-NAE-1). F_{terminal} had more bias and imprecision in the base case (TI-L-NAE-1), but the median RE and MARE values were lower than 25%. In the scenarios without ageing error, where the selectivity was time-invariant, time-varying double logistic (TI-DL-NAE-1, TV-DL-NAE-1), or time-varying logistic (TV-L-NAE-1), D_{final} , R_0 , and F_{terminal} also showed little bias and good precision (Figure 4, Table 2).

Strong positive bias (high median RE) and poor precision (high median MARE) in D_{final} , R_0 , and F_{terminal} were found in all scenarios with ageing errors (i.e. AE-1 scenarios), independent of the

selectivity pattern. The median RE and MARE values ranged between ~25 and 50% for D_{final} , ~80 and 100% for R_0 , and ~30 and 60% for F_{terminal} (Figure 4, Table 2).

In the presence of ageing error, the median RE and MARE values of D_{final} were greater when selectivity was double logistic (TI-DL-AE-1), than when logistic (TI-L-AE-1). When there was time-varying selectivity, i.e. logistic (TV-L-AE-1) or double logistic (TV-DL-AE-1), the bias and imprecision in D_{final} increased. D_{final} was most biased and imprecise in the scenario with time-varying double logistic selectivity, with the median RE and MARE values > 50% (Figure 4, Table 2).

In the presence of ageing error, R_0 estimates showed a significant positive bias (median RE near or above 100%) and poor precision (median $MARE > 75\%$), for all the time-invariant and time-varying selectivities, whether logistic (TI-L-AE-1 and TV-L-AE-1) or double logistic (TI-DL-AE-1 and TV-DL-AE-1) (Figure 4, Table 2). In scenarios with time-varying logistic (TV-L-AE-1) or double logistic selectivity (TV-DL-AE-1), R_0 showed a slightly lower positive bias and lower imprecision (Figure 4, Table 2). However, scenarios with time-invariant logistic (TI-L-AE-1) or double logistic (TI-DL-AE-1) selectivity showed little difference in bias and precision of the estimates.

F_{terminal} had higher positive bias and imprecision in scenarios with ageing error and time-invariant logistic selectivity (TI-L-AE-1), than in scenarios with time-invariant double logistic selectivity (TI-DL-AE-1). The median RE and $MARE$ values were close to 50 and 40%, respectively, with logistic and double logistic selectivity. Time-varying logistic (TV-L-AE-1) and double logistic (TV-DL-AE-1) selectivity increased the positive bias and imprecision in F_{terminal} , compared with scenarios with time-invariant selectivity (Figure 4, Table 2).

Independent of the selectivity function, scenarios where the data were generated with a time-varying catchability, but without ageing error (TI-L-NAE-2, TI-DL-NAE-2, TV-L-NAE-2, TV-DL-NAE-2), showed a slightly greater positive bias and imprecision in D_{final} and R_0 , than scenarios where the catchability was time-invariant (TI-L-NAE-1, TI-DL-NAE-1, TV-L-NAE-1, and TV-DL-NAE-1). On the contrary, the bias and imprecision of F_{terminal} was marginally lower when the data were generated with a time-varying catchability.

The positive bias of D_{final} increased marginally in those scenarios that combined ageing error with time-varying catchability (TI-L-AE-2, TI-DL-AE-2, TV-L-AE-2, and TV-DL-AE-2), compared with those that used time-invariant catchability (Figure 4). A lower precision also occurred in scenarios with time-varying catchability and ageing error (Table 2), but mainly in those scenarios where the selectivity was time-varying (TV-L-AE-2 and TV-DL-AE-2).

Time-varying catchability generated higher imprecision in R_0 in the scenarios with ageing error (TI-L-AE-2, TV-L-AE-2, and TV-DL-AE-2), compared with scenarios where the catchability was time-invariant (Figure 4). This was more marked when time-varying catchability interacted with time-varying selectivity (logistic and double logistic).

Time-varying catchability and ageing error (TI-L-AE-2, TI-DL-AE-2, TV-L-AE-2, and TV-DL-AE-2) produced a consistent pattern of bias in F_{terminal} . In particular, these scenarios presented a marginally lower positive bias and higher precision (lower $MARE$ values), compared with scenarios where the catchability was time-invariant (Figure 4, Table 2).

Correcting ageing error inside the estimation model

The ageing error correction decreased the positive bias and improved the precision of all parameter estimates (Figure 4, Table 2). In most scenarios (i.e. AEC), the estimates of D_{final} , R_0 , and F_{terminal} resulted in similar levels of bias and precision (median $MARE$ values were $< 26\%$) to the scenarios without ageing error (i.e. NAE scenarios). The ageing error correction improved the estimates under both time-invariant and time-varying selectivity scenarios (logistic and double logistic). In some cases, the estimates of D_{final} , R_0 , and F_{terminal} were less biased than in scenarios without ageing error (Figure 4).

In scenarios with logistic and double logistic selectivity (time-invariant and time-varying), the positive bias of D_{final} (the median of RE) decreased across all scenarios (TI-L-AEC-1, TV-L-AEC-1, TI-DL-AEC-1, and TV-DL-AEC-1), when the ageing error correction was used. The bias decreased from values above 25% to near zero (Figure 4). The precision of D_{final} was very similar between scenarios without ageing error (i.e. NAE scenarios) and those with ageing error correction (i.e. AEC scenarios), particularly in scenarios with logistic selectivity (Table 2).

In some scenarios, the D_{final} estimates were less biased and more precise when the ageing error correction was applied along with time-varying catchability. This mainly occurred in scenarios with the logistic and double logistic time-invariant selectivity (Figure 4, Table 2).

The positive bias in R_0 decreased from near 100%, in the presence of ageing error, to $< 25\%$, when the ageing error correction was applied (Figure 4). Applying the ageing error correction in the SCA also improved precision of the R_0 estimates (i.e. lower median $MARE$ values) across all selectivity scenarios (Table 2). In these scenarios, the median $MARE$ values were similar to the scenarios with correct age composition (i.e. NAE scenarios).

When the ageing error correction interacted with time-varying catchability (TI-L-AEC-2, TI-DL-AEC-2, and TV-L-AEC-2), R_0 showed a slight positive bias and decreased precision, compared with the scenarios where the catchability was time-invariant (TI-L-AEC-1, TI-DL-AEC-1, and TV-L-AEC-1; Figure 4, Table 2).

With the ageing error correction, the positive bias of F_{terminal} decreased from values near 50% (median value of RE) to values near zero. F_{terminal} was less biased when the ageing error correction was applied to scenarios with either time-invariant or time-varying selectivity (logistic and double logistic). Time-varying catchability had no substantial effect on F_{terminal} precision and bias, when the ageing error correction was applied in the SCA (Table 2).

Misspecification of selectivity

No ageing error

Figure 5 and Table 3 show the results for the scenarios where the selectivity was misspecified (i.e. the selectivity used in the OM was different from the selectivity assumed in the SCA) and the data were generated without ageing error and with either time-invariant or time-varying catchability. The misspecification of selectivity changed the bias and precision of D_{final} , R_0 , and F_{terminal} , compared with the parameter estimates when the same selectivity was used in both the OM and the SCA.

In scenarios where the data were simulated with time-invariant logistic selectivity, but the SCA assumed a time-invariant double logistic selectivity (TI-L-TI-DL-NAE-1), D_{final} estimates were similar to those estimated without selectivity misspecification [TI-L-TI-DL-NAE-1(*)] (Figure 5). However, R_0 and F_{terminal} showed lower bias and higher precision under the misspecification (Figure 5, Table 3). Moreover, R_0 and F_{terminal} exhibited marginally lower bias and more precision, even when the data were generated with time-varying catchability (TI-L-TI-DL-NAE-2).

When the data were generated with time-invariant double logistic selectivity and the SCA assumed time-invariant logistic selectivity (TI-DL-TI-L-NAE-1), D_{final} , R_0 , and F_{terminal} estimates were positively biased and less precise, compared with the scenarios without selectivity misspecification (Figure 5, Table 3). The addition of time-varying catchability generated even higher positive bias and lower precision in D_{final} and R_0 (TI-DL-TI-L-NAE-2).

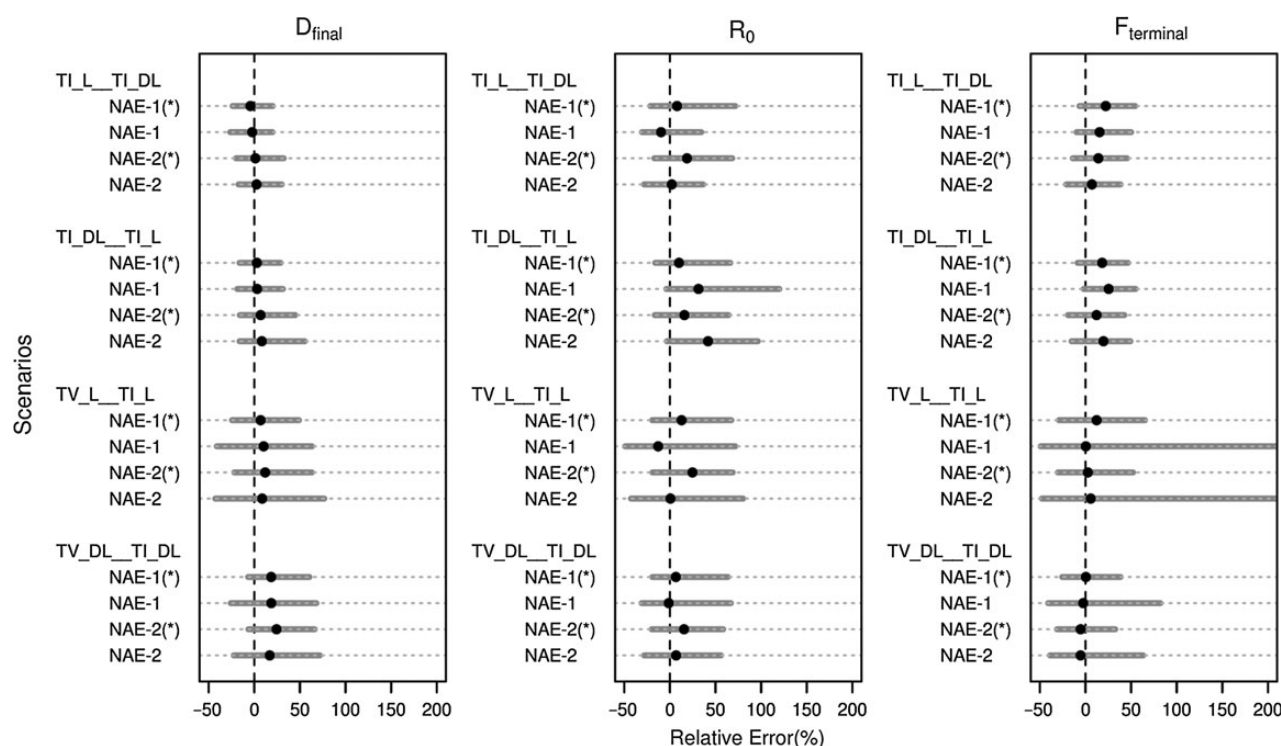


Figure 5. Results for misspecified selectivity models in the SCA. Median relative errors (black dots) and the central 90% confidence interval (grey line), for D_{final} , R_0 , and F_{terminal} , for the four cases and eight scenarios, where the selectivity was misspecified. Time-invariant logistic in OM and time-invariant double logistic in the SCA (TI_L_TI_DL), time-invariant double logistic in the OM and time-invariant logistic in the SCA (TI_DL_TI_L), time-varying logistic in the OM and time-invariant logistic in the SCA (TV_L_TI_L), and time-varying double-logistic in the OM and time-invariant double logistic in the SCA (TV_DL_TI_DL). NAE indicates that the data were generated without ageing error in the OM, and number 1 and number 2 indicate a time-invariant and time-varying catchability in the OM, respectively. The asterisks in parentheses represent the scenarios with correct selectivity specification (i.e. the selectivity function used in the OM was maintained in the SCA), given in parentheses in Table 3.

In the scenario where the true selectivity was time-varying logistic, but the SCA assumed a time-invariant logistic selectivity (TV-L_TI-L-NAE-1), the inter-quartile variability for D_{final} , R_0 , and F_{terminal} was larger, than in the scenario without selectivity misspecification. D_{final} was marginally positively biased, R_0 was underestimated, and F_{terminal} had a median RE value near zero but with the biggest inter-quartile range. All the parameter estimates were less precise when selectivity was misspecified (Figure 5, Table 3). Adding time-varying catchability improved the precision and accuracy of R_0 in the scenarios where the selectivity was misspecified (TV-L_TI-L-NAE-2); conversely, D_{final} and F_{terminal} were more imprecise (Figure 5, Table 3).

For the scenario where the selectivity was time-varying double logistic in the OM, but time-invariant double logistic in the SCA (TV-DL_TI-DL-NAE-1), the bias in D_{final} was similar to the scenario without selectivity misspecification, but with a bigger inter-quartile range (Figure 5); in contrast, R_0 was marginally less biased, and F_{terminal} was slightly underestimated. F_{terminal} showed higher inter-quartile variability and poor precision (Figure 5, Table 3). The use of time-varying catchability, with selectivity misspecification, generated similar estimates of D_{final} , R_0 , and F_{terminal} (TI-DL_TI-L-NAE-2).

Ageing error

Figure 6 and Table 4 show the results of the scenarios where the selectivity was misspecified and the data were generated with ageing error and with either time-invariant or time-varying catchability.

In these scenarios with ageing error, the misspecification either intensified the effects of the ageing error or masked the outcome, depending on the selectivity used in the OM and SCA.

For example, in the scenario where the true selectivity was time-invariant logistic, but the SCA assumed a time-invariant double logistic selectivity (TI-L_TI-DL-AE-1), higher positive bias and lower precision was seen in D_{final} , compared with the scenario without selectivity misspecification. Conversely, for R_0 and F_{terminal} , the effect of the ageing error was masked in the scenario with selectivity misspecification (i.e. a lower positive bias and higher precision) (Figure 6, Table 4).

In the scenario where the data were simulated with a time-invariant double logistic selectivity, but the SCA used time-invariant logistic selectivity (TI-DL_TI-L-AE-1), the estimates of D_{final} were marginally less biased and more precise, compared with the estimates without selectivity misspecification. In contrast, under the misspecification (TI-DL_TI-L-AE-1), the ageing error intensified the high positive bias and imprecision of R_0 and F_{terminal} (Figure 6, Table 4).

When the selectivity was time-varying logistic in the OM and time-invariant logistic in the SCA (TV-L_TI-L-AE-1), the ageing error generated slightly more biased and imprecise D_{final} estimates, compared with estimates without the selectivity misspecification. In contrast, for R_0 and F_{terminal} , the ageing error decreased the bias and increased the precision (lower median MARE values) under the misspecification (Figure 6, Table 4).

The use of time-varying double logistic selectivity in the OM, but a time-invariant double logistic selectivity in the SCA (TV-DL_TI-DL-AE-1), masked the ageing error effect. In particular, this

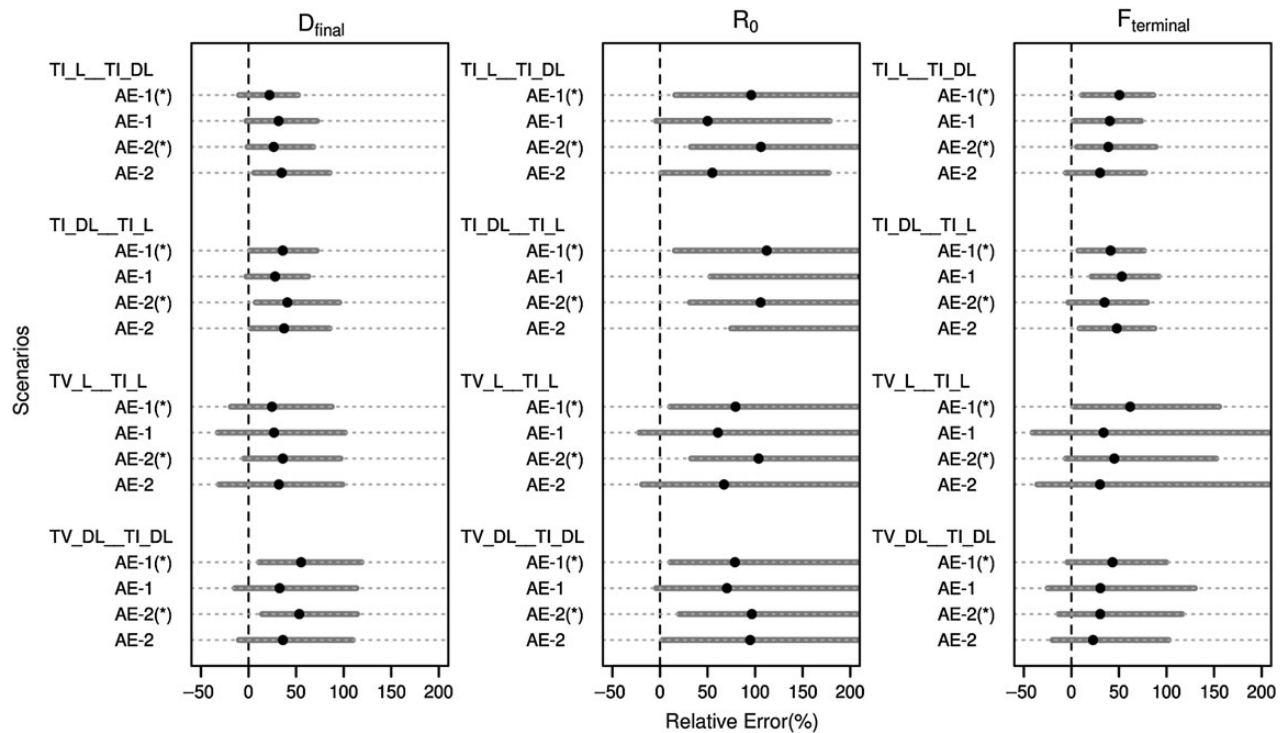


Figure 6. Results for misspecified selectivity models in the SCA. Median relative errors (black dots) and the central 90% confidence interval (grey line), for D_{final} , R_0 , and F_{terminal} , for the four cases and eight scenarios, where the selectivity was misspecified. Time-invariant logistic in OM and time-invariant double logistic in the SCA (TI_L_TL_DL), time-invariant double logistic in the OM and time-invariant logistic in the SCA (TI_DL_TL_L), time-varying logistic in the OM and time-invariant logistic in the SCA (TV_L_TL_L), and time-varying double-logistic in the OM and time-invariant double logistic in the SCA (TV_DL_TL_DL). AE indicates that the data were generated with ageing error in the OM, and number 1 and number 2 indicate a time-invariant and time-varying catchability in the OM, respectively. The asterisks in parentheses represent the scenarios with correct selectivity specification (i.e. the selectivity function used in the OM was maintained in the SCA), given in parentheses in Table 4.

generated an important decrease (more than 15%) in the positive bias and an increase in the precision of D_{final} , R_0 , and F_{terminal} , compared with the scenario with correctly specified selectivity (Figure 6, Table 4).

In some scenarios with ageing error, misspecification of selectivity, and time-varying catchability, the positive bias increased and precision decreased, for D_{final} and R_0 , while the positive bias and imprecision slightly decreased for F_{terminal} (Figure 6, Table 4).

Discussion

Effects of the ageing error on stock assessment parameters

Age composition data and fishery selectivity are key components within contemporary age-structured assessments. Yet, there is little research examining how ageing error and fishery selectivity assumptions interact to affect the quality of advice derived from stock assessment models. We set up a simulation-estimation approach to investigate how the ageing error and fishery selectivity assumptions interact under different scenarios, using Patagonian toothfish as a case study.

The ageing error generated by scale readings (i.e. underestimation of the age of the fish) of Patagonian toothfish generated substantial positive bias and imprecision in the estimation of D_{final} , R_0 , and F_{terminal} regardless of the assumptions about selectivity. Most importantly, our results showed that the ageing errors produced overly optimistic estimates of population status (D_{final}), over a range of SCA models, which could lead to overly optimistic TAC recommendations. Additionally, R_0 was the most positively biased and imprecise

parameter. Since, R_0 is a scale parameter, bias in R_0 could compromise the stock assessment estimates. Similar trends were found in the F_{terminal} estimates. These results agree with those reported by Liao *et al.* (2013), who found that F_{terminal} was overestimated by 19% when ageing error was introduced by a difference between scale and otolith age readings. In output control management strategies, F_{terminal} estimates need to be unbiased because they are important in setting catch limits and recovery plans, as well as in projecting future abundance under proposed management strategies.

Interaction between ageing error and time-invariant or time-varying selectivity

Different selectivity models were used in this simulation-estimation approach because it is difficult to know the true fishing selectivity. Therefore, we assessed the relative impact of combining different selectivity assumptions with the ageing error. We found that the imprecision and the positive bias in the parameter estimates varied depending on the selectivity type. For example, when ageing error was combined with time-invariant double logistic selectivity, D_{final} was more positively biased and less precise, than with time-invariant logistic selectivity. As a result, D_{final} produced the false perception of a less depleted stock. Conversely, F_{terminal} was less biased and slightly more precise when the ageing error interacted with the time-invariant double logistic selectivity. These differences were less pronounced in the estimates of R_0 .

The use of double logistic selectivity accentuated the problems due to the ageing errors. Double logistic selectivity is dome-shaped,

which assumes that the proportion of older fish caught by the fishing gear decreases with age. As a result, both the double logistic selectivity and the underestimation of fish age due to scale reading errors resulted in few older fish in the predicted numbers-at-age. Consequently, the stock assessment overestimated the stock status, D_{final} , and underestimated F_{terminal} . Dome-shaped selectivity can lead to biomass estimates with greater uncertainty, if this selectivity is misspecified in the estimation model (Crone *et al.*, 2013). This is a common problem because the true selectivity is unknown (Maunder and Piner, 2015).

Time-varying selectivity was included to evaluate how the ageing error interacts with fishery-dependent data. These sources of variability are expected to occur in most fisheries where cpue is the only abundance index, such as the Chilean Patagonian toothfish fishery.

The interaction between ageing error and time-varying selectivity (logistic and double logistic) generated higher positive bias and lower precision in the estimates of D_{final} and F_{terminal} . This reinforces the importance of including time-varying selectivity when simulating data in management strategy evaluations (e.g. closed-loop simulations) because real fishing selectivity is likely time-varying. Conversely, R_0 showed lower bias and higher precision, when time-varying selectivity interacted with the ageing error. This resulted in better estimates of R_0 , likely because the time-varying selectivity “absorbed” some of the noise from the ageing errors, while the time-invariant selectivity could not.

Using time-varying selectivity within a stock assessment has advantages and disadvantages. It provides greater flexibility to accommodate uncertainty, but increases the model complexity, by considerably increasing the number of estimated parameters, which could lead to overparameterization of the model (Linton and Bence, 2011). These issues could increase the relative error and imprecision for the D_{final} and F_{terminal} estimates. Nevertheless, Martell and Stewart (2014) suggested that in the absence of knowledge of selectivity, a time-varying selectivity should be assumed. In general, it is difficult to determine objectively when the selectivity changes in a fishery. Thus, in the absence of reliable information about changes in selectivity (e.g. for the Chilean Patagonian toothfish fishery), we tested the consequences of assuming a time-invariant selectivity when true selectivity is a time-varying function.

It must be emphasized to note that in the double logistic selectivity function (time-invariant and time-varying), the parameters that determined the right side of the selectivity curve (i.e. Ω_4 and Ω_5) generated a significant bias, mainly when they varied over time. Thus, they were fixed in the SCA. Similar to Linton and Bence (2011), we found that estimating the descending side of the curve was particularly problematic; the shape of the descending side of the curve could increase the uncertainty in the biomass estimates of the SCA.

The SCA performance was also evaluated when the data were generated with time-varying catchability and ageing error. Although the catchability was not the main objective of this study, we included it because time-varying catchability is common in fishery-dependent data and thus, for many current stock assessments. Generally, the results showed that the SCA performance decreased when ageing error combined with time-varying catchability. In particular, R_0 and D_{final} were marginally more positively biased and slightly less precise. However, the opposite effect occurred with the F_{terminal} estimates, where the estimates were slightly less biased and more precise. This implies that when the catchability varies over time, the ageing error more severely affects D_{final} and R_0 than F_{terminal} . Time-varying catchability should be expected in most

fishery-dependent data (Winters and Wheeler, 1985; Wilberg *et al.*, 2010). Factors such as changes in the abundance, the area inhabited by the stock, the environment, the fish behaviour or fishing gear, and the management regulations, among others, may cause catchability to be time-varying (Wilberg *et al.*, 2010). In this study, variability in the catchability was generated through a random walk. This method has been used in age-structured models to model gradual changes in catchability over time (e.g. Fournier *et al.*, 1998; Wilberg *et al.*, 2005, 2010). As with the time-varying selectivity, it is difficult to determine when catchability changes in a fishery. We used a small variation in catchability in the OM. However, we expect that if a higher variability in the time-varying catchability was combined with the ageing error, the performance of the SCA would have been even poorer. Thus, our results show that when D_{final} and R_0 are derived from fishery-dependent data, advice based on these parameters need to be more precautionary.

Interaction between ageing error and misspecification of selectivity

No ageing error

The inclusion of selectivity misspecification, affected the SCA performance, even in the absence of ageing error. When the OM used a time-invariant logistic selectivity and the SCA assumed a time-invariant double logistic selectivity, D_{final} , R_0 , and F_{terminal} were more precise and less biased. The effects on R_0 and F_{terminal} were more marked than for D_{final} . Similar results were found by He *et al.* (2011), who concluded that depletion was unbiased when the selectivity was incorrectly specified (i.e. logistic in the simulations and double logistic in the assessment model and *vice versa*). The improved estimation of R_0 and F_{terminal} likely occurred because the double logistic selectivity was able to absorb some of the observation error in the age composition of older fish. Also, the fishing mortality for older fish is different in the double logistic than logistic selectivity, and the SCA selectivity (double logistic) cannot buffer for the presence of older fish in the catch (logistic), therefore the fishing mortality decreases.

Conversely, when the OM used a time-invariant double logistic selectivity and the SCA assumed a time-invariant logistic selectivity, it increased the positive bias and imprecision in D_{final} , R_0 , and F_{terminal} . Similarly, Wang *et al.* (2014) found that R_0 (for *Thunnus obesus*) was estimated with high imprecision, when the selectivity was double logistic, but the assessment assumed a logistic function. We obtained similar results although Wang *et al.* (2014) used a more comprehensive estimation model with more abundance indices and only used length composition data. The positive bias in F_{terminal} also suggests that the SCA offsets the lack of older fish in the age composition by increasing the fishing mortality.

In the case when the selectivity was time-invariant in the SCA (logistic or double logistic) but time-varying (logistic or double logistic) in the OM, D_{final} and F_{terminal} showed low precision and high inter-quartile variability, while R_0 was generally estimated with higher precision. The selectivity misspecification affected the perception of the stock status, generating overly optimistic conditions. Under this selectivity misspecification, Crone *et al.* (2013) suggested using a more flexible selectivity function because changes in selectivity can produce biased estimates of management quantities and underestimate uncertainty.

Ageing error

The effect of ageing error on the parameters of interest may be exacerbated by a misspecification of the selectivity. In some cases, the

interaction between the ageing error and the selectivity misspecification increased the effect of the ageing error (increased bias and decreased precision), but in other cases, the effect of ageing error was masked.

For example, when the data came from the time-invariant logistic selectivity and the SCA assumed the time-invariant double logistic selectivity, D_{final} exhibited a marked positive bias. Punt *et al.* (2002), Yin and Sampson (2004), and Martell and Stewart (2014) have all shown that an incorrect assumption about the selectivity can lead to biased estimates of the spawning biomass and depletion. We found that the misspecification of time-invariant logistic selectivity, as time-invariant double logistic selectivity, can lead to even higher bias and imprecision when combined with ageing error. Of note, the effect of the selectivity misspecification on R_0 and F_{terminal} is more disturbing because it masked the effect of the ageing error, actually leading to less positive bias and more precision in the estimates. This probably occurred because, in the SCA, the time-invariant double logistic selectivity assumes that there are no older fish in the catch, which is similar to the effect generated by the ageing error. This situation can lead to overfishing because it assumes a larger stock than exists in reality.

When the data were generated using a time-invariant double logistic selectivity, but was a time-invariant logistic selectivity in the SCA, we observed the opposite effect to the previous case. Here, the effect of ageing error was slightly masked in D_{final} , but was accentuated in R_0 and F_{terminal} . The interaction between the misspecified selectivity and the ageing error particularly increased the positive bias in R_0 (median RE values > 200%). The lack of older fish generated by the ageing error and the time-invariant double logistic selectivity were likely offset by increasing the fishing mortality in the SCA.

In the case where the selectivity (logistic and double logistic) was time-invariant in the SCA but time-varying in the OM, this misspecification masked the effect of the ageing error on the parameter estimates. D_{final} , R_0 , and F_{terminal} all exhibited lower positive bias and higher precision, when compared with the scenarios where the selectivity was correctly specified. We found that ignoring the temporal changes in selectivity generally led to less biased and more precise parameter estimates, when the age composition was generated with ageing error.

Time-varying catchability, combined with misspecified selectivity, also affected the estimates of D_{final} and R_0 , whether ageing error was present or not. However, the effect was more pronounced when ageing error was present. In general, the interaction between time-varying catchability and misspecified selectivity led to an increase in the positive bias and imprecision of D_{final} and R_0 . On the contrary, the F_{terminal} estimates were less biased and more precise with and without ageing error.

Correcting ageing error inside the estimation model

This study also evaluated under which conditions correcting the ageing error could lead to less biased and more precise parameter estimates. We found that the correction reduced the average bias for D_{final} , R_0 , and F_{terminal} , regardless of the selectivity function used.

The results of this study suggest that when there is not enough information to quantify the ageing error (i.e. a small sample size of scale and otolith readings), it is still possible to perform an ageing error correction in the SCA. In general, ageing errors derived from scale and otolith readings can be corrected (e.g. Liao *et al.*, 2013). However, it is necessary to compare both structures from the same fish to correct for the bias produced by reading scales.

Unfortunately, our samples did not cover the entire range of older ages. This is probably the largest limitation in this work because we modelled the relationship between scales and otoliths using limited information for the older ages. However, we believe that the matrix used to simulate and correct the ageing error represents real errors in the age estimation of the Patagonian toothfish. In fact, in a study using Patagonian toothfish from South Georgia, older ages were consistently underestimated with scales, when compared with otolith readings (Ashford *et al.*, 2001); the bias was more severe than those used in our ageing error matrix.

Here, we tested the performance of our ageing error correction in a variety of scenarios using a simulation-estimation approach. We believe that the ageing error can be corrected using the procedure described in this study because without this correction, the SCA produced a more optimistic stock status than when the stock was evaluated with the ageing error correction.

Implications for Chilean Patagonian toothfish assessment

There are many studies that show how the ageing error has contributed to the overexploitation of fish populations (e.g. Chilton and Beamish, 1982; Campana *et al.*, 1990; Smith *et al.*, 1995). The age underestimation produced by the scale readings is likely to generate biased estimates in the current Chilean Patagonian toothfish stock assessment, if the ageing error correction is not applied to this stock.

Considering that fishery selectivity is unknown usually, especially when there is only fishery-dependent information, it is not recommended to assume a time-invariant selectivity function. Moreover, our results show that the use of a time-invariant dome-shaped selectivity is even more problematic. We showed that this selectivity may increase the effect of ageing error on the determination of the stock status. We believe that dome-shaped selectivity should not be used when there is only one fishing gear, as is true in the Chilean Patagonian toothfish fishery. Our results show that using time-varying logistic selectivity in the assessment model may produce less biased parameter estimates and more conservative results.

Additionally, we showed that the time-varying catchability also produced bias in the estimated parameters, mainly when it interacted with ageing error. However, it is highly probable that the catchability is time-varying in this fishery because the only available abundance index is the cpue.

We believe that by including both a time-varying logistic selectivity and the ageing error correction, the stock assessment can produce more reliable results for determining catch limits and evaluating management strategies in the Chilean Patagonian toothfish fishery.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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Appendix A. Age-structured operating model (OM)

This appendix presents the equations for the age-structured OM implemented in R. The model notation and parameters are given in Table 1 (see paper). The equations are presented in Table A1.

Life history schedules

The length-at-age (l_a) was modelled following a von Bertalanffy growth model (A1.1) and the weight-at-age (w_a) was obtained from the weight–length relationship (A1.2). The maturity-at-age (A1.3) was used to define the proportion of the mature population at each age. A logistic maturity-at-age (m_a) function was applied.

Stock–recruitment relationship

The unfished equilibrium spawning biomass per recruit (ϕ) was modelled as shown in Equation (A2.1). The unfished recruitment (R_0) was defined as shown in Equation (A2.2).

The parameters a (A2.3) and b (A2.4) are the Beverton–Holt stock–recruitment relationship parameters.

Basic abundance dynamics

The OM creates the population dynamics with a continuous fishing mortality, where the number of fish in age group a , at the start of each year t , was calculated as shown in Equation (A3.1). The abundance-at-age 1 ($N_{a,t}$) corresponds to annual recruitment of age-1 (A3.2), which is lognormally distributed about a Beverton–Holt stock–recruitment relationship, parameterized as a function of steepness (h). The spawning-stock biomass (SSB_t) of fish in age group a , at the start of each year t , was calculated as shown in Equation (A3.3).

Initial conditions

The initial conditions were modelled with Equations (A4.1–A4.3). Equation (A4.1) represents the number of fish in age group a in the initial year (year 1). In this Equation (A4.1), random recruitment deviations were included. Equation (A4.2) gives the number of fish in the plus group in year 1. The spawning biomass of fish in age group a in year 1 was calculated in Equation (A4.3).

Fishery selectivity

Time-invariant (A5.1) or time-varying (A5.2) logistic and time-invariant (A5.3) or time-varying double logistic (A5.4) selectivity functions were assumed for the fishery. For time-varying logistic selectivity (A5.2), Ω_{1t} (age 50% of selectivity) varied year to year, following a random walk with autocorrelation. The initial value (year 1) was drawn randomly from a standard normal distribution $\delta_i \sim N(0, \sigma_{\Omega_1}^2)$. For years 2–24, the random walk with autocorrelation was applied following Equation (A5.5). A logit transformation was applied to the r_{5t} values to get values between 0 and 1. Then, Ω_{1t} values were allowed to vary between the lower (L_{Ω_1}) and upper bounds (U_{Ω_1}) of Ω_{1t} as Equation (A5.6). For time-varying double logistic selectivity (A5.4), the Ω_{3t} (Inflection 1) and Ω_{4t} (Inflection 2) parameters varied year to year following a random walk with autocorrelation. The same procedure was applied for the time-varying logistic and double logistic selectivity, but for double logistic selectivity, the random walk was applied to both Ω_{3t} and Ω_{4t} .

Fishery catch

The catch of fish of age a during year t (in numbers) was determined using the Baranov catch equation (A6.1). The biomass caught by the fishery was calculated as shown in Equation (A6.2). Observed catch-at-age data were simulated using random draws from a multinomial distribution with a sample size of 800 (A6.5). For the first 18 years of the fishery, the observed catch-at-age was derived from scale-based age readings and, for the final 6 years, the observed catch-at-age was derived from otolith-based age readings (A6.6–A6.7).

Fishery-dependent information

A fishery-dependent index (cpue) was generated (A7.1–A7.2). The coefficient of catchability was generated in the OM, as either a constant parameter (q) or as a random walk process (q_t), depending on the cases and scenarios. When a time-varying catchability was used

Table A1. Patagonian toothfish fishery-operating model for generating age-structured population dynamics, indices of relative abundance, and age-proportion data.

A1 Life history schedules	
A1.1	$l_a = l_\infty \times (1 - \exp^{(-k(a-a_0))})$
A1.2	$w_a = cl_a^d$
A1.3	$m_a = \frac{1}{1 + \exp[-\log(19)(a - a_{50})/(a_{95} - a_{50})]}$
A2 Stock – recruitment relationship	
A2.1	$\phi = \sum_{a=1}^{A-1} \exp^{-M(a-1)} m_a w_a + \frac{\exp^{-M(A-1)} m_A w_A}{1 - \exp^{-M}}$
A2.2	$R_0 = \frac{B_0}{\phi}$
A2.3 – A2.4	$a = \frac{4hR_0}{B_0(1-h)} \quad b = \frac{5h-1}{B_0(1-h)}$
A3 Basic abundance dynamics	
A3.1	$N_{a,t} \begin{cases} N_{a,t} & a = 1 \\ N_{a-1,t-1} \exp^{-M+F_{t-1}S_{a-1}} & 1 < a < A \\ N_{A-1,t-1} \exp^{-M+F_{t-1}S_{A-1}} + N_{A,t-1} \exp^{-M+F_{t-1}S_A} & a = A \end{cases}$
A3.2	$N_{1,t} = \frac{a \text{ SSB}_{t-1}}{1 + b \text{ SSB}_{t-1}} \exp^{(\omega_t - 0.5\sigma_R^2)} \quad \omega_t \sim N(0, \sigma_R^2)$
A3.3	$\text{SSB}_t = \sum_{a=1}^A N_{a,t} m_a w_a$
A3.4	$\text{VB}_t = \sum_{a=1}^A (N_{a,t} S_a w_a)$
A4 Initial condition	
A4.1	$N_{a,1} = R_0 \exp^{-M(a-1)} \exp^{(\omega_t - 0.5\sigma_R^2)} \quad \omega_t \sim N(0, \sigma_R^2) \quad 1 \leq a \leq A-1$
A4.2	$N_{A,1} = \frac{NA - 1, 1 \exp^{[-M(A-1)]}}{1 - \exp^{-M}}$
A4.3	$\text{SSB}_{a,1} = \sum_{a=1}^A N_{a,1} m_a w_a$
A5 Fishery selectivity	
A5.1	$S_a = \frac{1}{1 + \exp^{[-\log(19)(a - \Omega_1)/(\Omega_2 - \Omega_1)]}}$
A5.2	$S_{a,t} = \frac{1}{1 + \exp^{[-\log(19)(a - \Omega_{1t})/(\Omega_2 - \Omega_{1t})]}}$
A5.3	$S_a = \frac{1/(1 + \exp^{[-\Omega_5(a - \Omega_3)])} [1 - (1 + \exp^{[-\Omega_6(a - (\Omega_3 + \Omega_4))])])]}{\text{MAX}_a(\text{num}_a)}$
A5.4	$S_{a,t} = \frac{1/(1 + \exp^{[-\Omega_5 \times (a - \Omega_{3t})])} [1 - (1 + \exp^{[-\Omega_6(a - (\Omega_{3t} + \Omega_{4t}))])])]}{\text{MAX}_a(\text{num}_a)}$
A5.5	$rs_t \begin{cases} \delta_1 & t = 1 \\ \rho_{\Omega_1} rs_{t-1} + (1 - \rho_{\Omega_1}) \delta_t & \delta_t \sim N(0, \sigma_{\Omega_1}^2) \\ & t > 1 \end{cases}$
A5.6	$\Omega_{1t} = L_{\Omega_1} + rs_t (U_{\Omega_1} - L_{\Omega_1})$
A6 Fishery catch	
A6.1	$C_{a,t} = N_{a,t} S_{a,t} F_t \frac{(1 - \exp^{(-M - S_{a,t} F_t)})}{(M + S_{a,t} F_t)}$
A6.2	$C_w = \sum_{a=1}^A C_{a,t} w_a$
A6.3 – A6.4	$\tilde{C}_t = \sum_a C_{a,t} \quad \tilde{P}_{a,t} = C_{a,t} / \tilde{C}_t$
A6.5	$P_{a,t} \sim MN(800, \tilde{P}_{a,t})$
A6.6 – A6.7	$\bar{P}_{a,t(1989-2006)} = P_{a,t} \times P(a' a) \quad \bar{P}_{a,t(2007-2012)} = P_{a,t} \times E(a' a)$
A7 Fishery-dependent information	
A7.1	$\text{cpue} = q \text{ VB}_t \exp^{(\varepsilon_t - 0.5\sigma_T^2)} \quad \varepsilon_t \sim N(0, \sigma_T^2)$
A7.2	$\text{cpue} = q_t \text{ VB}_t \exp^{(\varepsilon_t - 0.5\sigma_T^2)} \quad \varepsilon_t \sim N(0, \sigma_T^2)$
A7.3	$rq_t \begin{cases} \varphi_1 & t = 1 \\ \rho_q rq_{t-1} + (1 - \rho_q) \varphi_t & \varphi_t \sim N(0, \sigma_q^2) \\ & t = 2, \dots, T \end{cases}$
A7.4	$r_t = rq_t \sim t$
A7.5	$q_t = \exp(rq_t + rs_t)$

Table B1. Likelihood function for fitting the SCA model to simulated index and catch-at-age-observations.

Estimated parameters B1.1	$\Theta_1 = (R_0, \bar{R}, \{w_t\}_{t=1}^{T-1}, \bar{F}, f_t, \Omega_1, \Omega_2, \Omega_3, \Omega_5 \delta_t, q)$
Maximum likelihood estimates B1.2 (Catches)	$L_1 = n_c \ln(\sigma_c) + \frac{1}{2\sigma_c^2} \sum_{t=1}^{t=T} \ln \left(\frac{C_t}{\bar{C}_t} \right)^2$
B1.3 (abundance index, cpue)	$L_2 = n_l \ln(\sigma_l) + \frac{1}{2\sigma_l^2} \sum_{t=1}^{t=T} d_t^2$ $d_t = z_t - \bar{z}; \quad \bar{z} = \frac{\sum_{t=1}^{t=T} z_t}{n_l}; \quad z_t = \ln(\text{cpue}_t) - \ln(\text{VB}_t); \quad q = \exp(\bar{z})$
B1.4 (Age composition)	$L_3 = \sum_{t=1}^{t=T} \sum_{a=1}^{a=A} n_t [\hat{P}_{a,t} \ln(\bar{P}_{a,t})], \quad n_t = 200$
B1.5 (Recruitment deviations and mean recruitment)	$L_4 = n_\omega \ln(\sigma_R) + \frac{1}{2\sigma_R^2} \sum_{t=1}^{t=T-1} \omega_t^2; \quad \omega_t = \ln(\bar{R} \exp^{\omega t}) - \ln(R'_t); \quad (R'_t) = \text{Beverton and Holt}$
B1.6 (Fishing mortality estimates)	$P_1 = \frac{1}{2\sigma_f^2} \sum_{t=1}^{t=T} f_t^2; \quad \bar{F} e^{f_t}; \quad f_t, \sum_{t=1}^{t=T} f_t = 0; \quad \sigma_t = 0.01 \text{ if initial phase, } 0.4 \text{ otherwise}$
B1.7 ^a (Deviates for fishing selectivity)	$P_2 = \frac{1}{2\sigma_\delta^2} \sum_{t=1}^{t=T} \delta_t^2; \quad \delta_t = \ln(\Omega_{1t}) - \ln(\Omega_{1t+1}); \quad \Omega_{1t} = \Omega_{1t-1} e^{\delta_{t-1}}$
Objective function B1.8 (Total likelihood)	$L_T = \sum_k L_k + \sum_l P_l$

^aLikelihood function for selectivity parameters that varied following a random walk: Ω_1, Ω_3 . The term δ_t represents the normal deviates used in the random walk process.

Table B2. Ageing correction procedure performed in the SCA model.

Ageing error correction procedure B2.1	$C_{a,t(\text{scales})} = N_{a,t} S_{a,t} F_t \frac{(1 - \exp^{(-M - S_{a,t} F_t)})}{(M + S_{a,t} F_t)} \times T(P_{\text{MLE}}(a' a)) \quad t = 1984, \dots, t = 2006$
B2.2	$C_{a,t(\text{otoliths})} = N_{a,t} S_{a,t} F_t \frac{(1 - \exp^{(-M - S_{a,t} F_t)})}{(M + S_{a,t} F_t)} \quad t = 2007, \dots, T = 2012$ $\hat{P}_{t,a} = \frac{C_{a,t}}{\sum_t C_{a,t}} \quad t = 1984, \dots, T = 2012$

in the data generation process, the parameter varied year to year following a random walk with autocorrelation. The initial value (year 1), in log-space to avoid negative values, was drawn randomly from a standard normal distribution $[\varphi_t \sim N(0, \sigma_\varphi^2)]$. For years 2–24, it was modelled using the autocorrelation random walk function, as Equation (A7.3). Finally, a linear regression (r_t) was applied and the residuals (rs_t) were taken to obtain q_t , using Equations (A7.4) and (A7.5).

Appendix B: SCA model

The life history schedules, stock–recruitment relationship, initial condition, basic abundance dynamics, fishery selectivity, and fishery catch were modelled as in the OM, except for the catchability parameter (q), which was a time-invariant parameter in the SCA model (see Appendix A; Table A1). The model notation and parameters are given in Table 1 (see paper).

In the time-varying selectivity function, the parameters estimated were the age 50% of selectivity (Ω_{1t}) of the logistic selectivity, and the inflection 1 (Ω_{3t}) and slope 1 (Ω_5) of the double logistic selectivity and the annual deviations for Ω_{1t} and Ω_{3t} ($\delta_t \sim N(0, \sigma_\delta^2)$).

The maximum likelihood and log-likelihood estimates from the SCA are given in Table B1.

Ageing error correction procedure

The $P_{\text{MLE}}(a'|a)$ matrix with the maximum likelihood estimation (MLE) of y_{max} and m was used to correct the ageing error. The equations are presented in Table B2. The correction of the error involved multiplication of the estimated age proportion, for the years 1984–2006, by the transpose (T) of the $P_{\text{MLE}}(a'|a)$ matrix (B2.1). After the “corrected” catch-at-age was obtained, the proportion-at-age was calculated following Equation (B2.2). This “corrected” age composition (proportion) matrix was input into the multinomial likelihood in the objective function in the SCA model [Table B1, Equation (B1.4)].

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