



Variation in growth among individuals and over time: A case study and simulation experiment involving tagged Antarctic toothfish



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ABSTRACT

Organisms in the marine environment are likely to exhibit variation in growth rates among individuals, and this variation may be persistent (particular individuals growing faster/slower throughout their entire lifetime) or transient (particular individuals growing faster in one year than another year). Understanding variation in growth is necessary when interpreting data regarding size (length or weight) in population models, or when estimating growth given data for tagged individuals. In this study, we explicitly model persistent and transient variation in growth rates among individuals in a wild marine population of Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, in addition to sex-specific differences in average growth rates. The model is implemented using maximum marginal likelihood estimation and validated using a simulation study. The code is distributed as a publicly available package *TagGrowth* in the R statistical environment. Using simulated data, we show that we can accurately estimate parameters representing the magnitude of persistent and transient variation in growth rates, and that parameters estimated in these models are reasonably precise given the case study sample sizes (315 individuals tagged and recaptured over 10 years). The case study application suggests that transient variation among individuals accounts for up to half of the total variability in Antarctic toothfish. We conclude by recommending further research to additionally estimate temporal and spatial variation in growth rates. Estimating the relative magnitude of multiple sources of growth variation will improve our ability to assess the sensitivity of existing population models to growth variation, as well as to understand the range of variation exhibited by wild marine populations.

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1. Introduction

Variation in growth rates for fish populations has been discussed by fisheries scientists for over 100 years. Growth in fishes arises from complex behavioral trade-offs for each individual in a population. Growth (measured as an increase in standard length) arises from the allocation of energy between increased size (length) and increased condition (i.e., weight at length). Individuals can also increase their rate of energy acquisition via increased foraging activity, but increased foraging may also change the risk of predation. Environmental conditions modify the potential for growth, as well as the trade-offs faced by individual fish. For example, increases in water temperature are associated with increased activity levels but also increased energetic demands for maintaining

existing body tissue, such that the net effect of changing temperature on growth may vary among individuals (Shelton et al., 2013). Similarly, changes in survival rates (via fishery harvest) may favor earlier maturation, thus affecting growth by altering the relative allocation of energy between growth and reproduction.

Organisms in the marine environment are likely to exhibit variation in growth rates among individuals, and this variation may be persistent (particular individuals growing faster/slower throughout their entire lifetime) or transient (particular individuals growing faster in one year than in another year). Many recent studies of captive or wild populations have demonstrated persistent differences in behavioral or phenotypic traits among individuals (termed differences in “personality”, Wolf and Weissing, 2012). Persistent differences in activity level or tolerance of predation risk (i.e., a tendency to forage in high vs. low-quality habitat) will likely lead to persistent differences in growth rates among individuals. Subsequently, persistent differences in growth rate, combined with size-selective harvest targeting larger individuals,

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can result in older individuals being composed primarily of slow-growing individuals (termed “Rosa Lee’s Phenomenon”), and has been demonstrated to occur in small-lake mesocosm experiments (Biro and Post, 2008). In this way, failure to account for persistent differences in growth rate can lead to biased estimation of average growth rates in wild populations; population dynamics models are increasingly being developed to account for these effects (Taylor and Methot, 2013).

Individuals are also likely to experience transient variation in growth rates. Transient variation could be caused by many different processes including movement between warmer/colder ambient temperatures (and hence transient variation in metabolic rates), periodic access to improved feeding (Armstrong and Schindler, 2011), and year-specific changes in the allocation of resources between growth and reproduction (Jørgensen and Fiksen, 2006).

Finally, sex-specific differences in behavior can result in differences in average growth rates between males and females (Biro and Sampson, 2015). Sex-specific differences in growth rate are commonly included in population models for marine species (Methot and Wetzel, 2013). We therefore hypothesize that most marine populations will have multiple sources of variability in individual growth rates, including:

1. Persistent variation among individuals (i.e., some individuals grow faster or to a larger size than others),
2. Transient variation over time for a given individual (i.e., individuals will have spurts and drops in growth rates),
3. Variation in average growth rates between females and males.

Estimation of growth rates among individuals and over time therefore requires partitioning variation among multiple potential types, and mixed-effects models are generally advocated for this task (Thorson and Minto, 2015). Mixed-effects models partition variation among multiple sources by estimating true size at age as a latent variable, which is integrated across while estimating growth parameters. True growth rates can therefore vary among individuals, and the magnitude of this variation can be explained by multiple putative sources. Hierarchical models are increasingly advocated as a strategy to partition variability into multiple sources, and hence to interpret which source of variance is worth further study (Gelman, 2005; Larsen et al., 2001). We therefore believe that partitioning variation in growth rates among multiple possible factors can help to guide subsequent, mechanistic research regarding potential drivers for the type of variability that is identified as having greatest magnitude.

Growth rates in natural populations are generally estimated using capture-mark-recapture (CMR) models. In CMR studies for marine fishes, thousands of individuals are typically captured and marked with a persistent and unique tag, and then measured and released. If a tagged individual is recaptured, it is often killed and its age at recapture identified via analysis of hard parts (e.g., otoliths). Given the known time between capture and recapture, its size and age at both times can be calculated. This study design allows a model for growth increments to be fitted to size and age data for two times for each individual in a data set. Many studies have examined the impact of persistent or transient growth variation on estimation of growth patterns using CMR data for wild marine populations (Francis, 1988; Sainsbury, 1980). However, few studies have explicitly modeled multiple sources of variability in growth rates. Exceptions include Shelton et al. (2013), which modeled persistent, temporal, and transient variation in growth rates in the analysis of data from a growth experiment for steelhead trout, and Vincenzi et al. (2014), which modeled persistent variation in growth rates arising from environmental and density-dependent influences.

In this study, we present a model for partitioning variation in growth into persistent, transient, and sex-specific factors, and parameters are then estimated using maximum marginal likelihood methods. The code is distributed as a publicly available package *TagGrowth* in the R statistical environment (<https://github.com/quantifish/TagGrowth>), and is illustrated using CMR data for Antarctic toothfish (*Dissostichus mawsoni*). Using these data, we show that we can accurately estimate parameters for a model that includes multiple sources of individual variation in growth, and that estimates are reasonably precise given a feasible number of individual recaptures (250 or more). Our case study application suggests that transient variation over time accounts for up to half of the total variability in Antarctic toothfish in the Ross Sea.

2. Methods

We start with the specialized von Bertalanffy growth function:

$$\frac{dL}{dt} = a - kL \quad (1)$$

where dL/dt is change in length L as a function of time t , a scales with energy acquisition, and k represents metabolic upkeep costs. Persistent variation among individuals can be estimated by treating each individual's demographic parameters as a random effect that arises from a population-level distribution (Thorson and Minto, 2015). Here, we treat average metabolic upkeep costs k_i as varying among individuals (where subscript i signifies the upkeep rate for the i -th individual), due to differences in ambient temperature, intrinsic variation in activity levels, and other factors:

$$k_i = \mu_k \exp(\epsilon_i^k) \quad (2)$$

where $\epsilon_i^k \sim N(0, \sigma_k^2)$, μ_k is the median k_i among individuals in the population, and σ_k^2 is the variance of individual upkeep cost deviations (ϵ_i^k).

Individuals that are more highly active may obtain more food (increased a) and simultaneously have greater upkeep costs (increased k). Following Snover et al. (2005) and Shelton et al. (2013), we include this association via the following equation:

$$a_i = \gamma k_i^\psi \quad (3)$$

where ψ determines whether upkeep costs (k_i) and energy acquisition rate (a_i) are highly correlated ($\psi = 1$) or independent among individuals ($\psi = 0$), and γ controls the average energy acquisition rate among individuals.

We also assume that environmental conditions experienced by each individual will vary over time, such that each individual will have “transient” variation over time in their upkeep costs (k_i), in turn affecting their access to food (a_i). In particular, we assume that upkeep costs for a given individual (i) for a short time interval (t) can be approximated by a constant value ($k_{i,t}$), which will vary around the average value for this individual (k_i). Integration then yields:

$$L(t + \Delta t) = L(t) \exp\left(-\frac{k_i}{n_\Delta} \Delta t\right) + \left(\frac{k_i}{n_\Delta}\right)^{\psi-1} \times \left(1 - \exp\left(-\frac{k_i}{n_\Delta}\right)\right) \frac{\gamma}{n_\Delta} \sum_{j=0}^{\Delta t-1} \exp\left(-\frac{k_i}{n_\Delta} j\right) + z_{\Delta t, i} \quad (4)$$

where

$$z_{\Delta t, i} \sim N\left(0, \sigma_z^2 \left[\left(\frac{k_i}{n_\Delta}\right)^{\psi-1} \left(1 - \exp\left(-\frac{k_i}{n_\Delta}\right)\right)\right]^{2\Delta t-1} \sum_{j=0}^{\Delta t-1} \exp\left(-2\frac{k_i}{n_\Delta} j\right)\right)$$

where Δ_t is the number of time-periods (weeks) elapsed between two times (e.g., tagging and subsequent recapture) and n_Δ is the number of time-periods per year (52.15), such that k_i is the Brody growth coefficient (with units years^{-1}), and σ_z is the magnitude of transient growth variation (see Appendix A in Supplementary material for derivation of $z_{\Delta_t,i}$, summarized from Shelton et al., 2013). In this study, we use a time interval of one week (7 days). We confirm that results are similar for other small time intervals (i.e., days or months), but found that an annual time interval resulted in parameter estimates that resulted in growth schedules that were biased high relative to the simulated (“true”) values. We assume that all age-0 individuals have a length $L_{0,s}$ that differs between males ($s=0$) and females ($s=1$), and estimate length-at-birth for each sex. Eq. (4) can then be used to calculate the predicted length at first capture $L(t_1)$ and upon recapture $L(t_1 + t_2)$, where t_2 is the time between first tagging and recapture (time at liberty), and $t_1 + t_2$ is the age at recapture as determined from conventional ageing methods. We assume that individual age at the time of recapture is read without error, although future research could include ageing error by treating true age as a random effect (Cope and Punt, 2007; Punt et al., 2008).

The observed length for each individual upon first tagging $L_{\text{obs}}(t_1)$ and upon recapture $L_{\text{obs}}(t_1 + t_2)$ is assumed to follow a normal distribution with a fixed coefficient of variation (c.v., representing observation error caused by at-sea length measurements) given the estimated length at that age $L(t)$:

$$L_{\text{obs}}(t) \sim N(L(t), \sigma_{\text{obs}}^2) \quad (5)$$

where $\sigma_{\text{obs}} = c_{\text{obs}}L(t)$, and c_{obs} is the c.v. of observed growth.

2.1. Estimation

We estimate the value of fixed effects in this model (L_0 , μ_k , σ_k , γ , σ_z , c_{obs}) using maximum marginal likelihood while integrating across the probability of all random variables representing persistent and transient variation among individuals (Thorson and Minto, 2015). Parameter estimation is conducted using Template Model Builder (TMB; Kristensen, 2014; Kristensen et al., 2015; available from: <https://github.com/kaskr/adcomp>) software called from the R statistical environment (R Core Development Team, 2013) and all code necessary for replicating the case study and simulation experiment are publicly available (<https://github.com/quantifish/TagGrowth>; Appendix B in Supplementary material). The marginal likelihood is then maximized using conventional nonlinear minimization tools in R, while using the gradient of the marginal likelihood with respect to fixed effects as calculated by TMB. Standard errors are then estimated using the inverse of the matrix of second derivatives of the marginal likelihood with respect to fixed effects, evaluated at their maximum likelihood values (termed the “information matrix”) via the delta-method.

After fixed effects have been estimated, the median asymptotic length (μ_{L_∞}) for individuals in the population can be calculated as:

$$\mu_{L_\infty} = \gamma \mu_k^{\psi-1} \quad (6)$$

which is obtained by setting Eq. (1) equal to zero, substituting in Eq. (3), and rearranging. Readers are referred to Shelton et al. (2013) for an expanded model that also incorporates variability in average energy acquisition rates (γ) for all individuals in a given time period. All of the variables used in this paper are outlined in Table 1.

2.2. Simulation

A simulation study was done to evaluate potential bias and precision of different model structures and to ensure that the model performs well given data similar to those observed in the actual

Table 1

List and definition of symbols used in the text and equations with their units.

Parameter name	Symbol	Units
The number of time periods per year	n_Δ	–
The hypothetical length at which time $t=0$	$L_{0,s}$	cm
Anabolic rate	a_i	–
Energy expenditure rate (“Brody growth coefficient”)	$\mu_{k,s}, k_{i,s}$	years^{-1}
Anabolism coefficient	γ_s	years^{-1}
Allometric scaling of anabolism and energy expenditure	ψ	–
Time variation	$z_{\Delta_t,i}$	cm
Asymptotic maximum length	$\mu_{L_\infty,s}, L_{\infty,i,s}$	cm
The hypothetical time at which $L(t)=0$	$t_{0,s}$	years
Observation coefficient of variation (c.v.)	c_{obs}	–
Energy expenditure rate standard deviation	$\sigma_{k,s}$	years^{-1}
Time variation standard deviation	σ_z	cm
Data	Symbol	Units
Time interval	Δ_t	weeks
Length at time t	$L(t)$	cm
Indices	Symbol	Units
Individual	i	–
Time	t	weeks
Sex	s	–

Antarctic toothfish data set. This simulation study involved two separate experiments. The first experiment was regarding model performance given variation in the true data-generating process. Four different scenarios were simulated in this experiment including: no random-effects, random-effects for persistent individual variation in upkeep costs for each sex ($k_{i,s}$ only), transient variation in growth ($z_{\Delta_t,i}$ only), and both persistent and transient variation in growth (both $k_{i,s}$ and $z_{\Delta_t,i}$). In each of these simulated scenarios a sample size (n) of 315 individuals was used (the same sample size as the toothfish data set). The second simulation experiment was regarding model performance given variation in sample sizes. We therefore conducted a power analysis for the scenario including both persistent and transient variation in growth where data were simulated for 50, 100, 250 and 500 recaptured individuals. In total, we simulated 8 scenarios among 2 simulation experiments.

In each simulation scenario, we take average age at length zero ($t_{0,s}$), the Brody growth coefficient (k_s), and asymptotic maximum length ($L_{\infty,s}$) from Dunn et al. (2006) and used them to derive the values of the length at birth ($L_{0,s}$) and average energy acquisition rate (γ_s) parameters used in the simulation study (Table 2). These can be calculated as:

$$L_0 = L_\infty \left(1 - \exp \left(\frac{kt_0}{n_\Delta} \right) \right) \quad (7)$$

and

$$\gamma = \frac{k}{n_\Delta} L_\infty / \left(\frac{k}{n_\Delta} \right)^\psi \quad (8)$$

The length at birth ($L_{0,s}$), average upkeep cost ($\mu_{k,s}$), magnitude of persistent variation in growth ($\sigma_{k,s}$) and average energy acquisition rate (γ_s) parameters were all assumed to be sex-specific in the simulation study, while the magnitude of transient variation in growth (σ_z) and the magnitude of error when measuring length (c_{obs}) were not (Table 2). The c.v. of observed growth (c_{obs}) was set at the value in Dunn et al. (2006) in those scenarios with no random-effects. In the remaining scenarios, the c.v. of observed growth (c_{obs}), magnitude of persistent variation among individuals ($\sigma_{k,s}$) and magnitude of transient variation (σ_z) were set at values that resulted in reasonable variation in individual length trajectories (Table 2). In the case study we fixed $\psi=0$ and discuss our reasons further below. We therefore chose to fix $\psi=0$ in the simulation experiment as well.

Table 2
Compilation of sex-specific growth parameters as previously estimated by Dunn et al. (2006), used in all simulation scenarios, or varying among simulation scenarios.

Parameter	Units	Female	Male
Previous estimates of parameters (Dunn et al., 2006)			
$t_{0,s}$	years	0.021	-0.256
k_s	years ⁻¹	0.090	0.093
$L_{\infty,s}$	cm	180.20	169.07
c.v.	–	0.102	0.102
Parameter values fixed in all simulation scenarios			
$L_{0,s}$	cm	-0.3409	3.9777
$\mu_{k,s}$	years ⁻¹	0.090	0.093
γ_s	years ⁻¹	16.218	15.724
Parameter values that vary among simulation scenarios			
Scenario 1—“No variation”			
c_{obs}	–	0.102	0.102
$\sigma_{k,s}$	–	–	–
σ_z	–	–	–
Scenario 2—“Variation in $k_{i,s}$ ”			
c_{obs}	–	0.05	0.05
$\sigma_{k,s}$	–	0.1	0.2
σ_z	–	–	–
Scenario 3—“Variation in $z_{\Delta t,i}$ ”			
c_{obs}	–	0.05	0.05
$\sigma_{k,s}$	–	–	–
σ_z	–	0.3	0.3
Scenario 4—“Variation in $k_{i,s}$ and $z_{\Delta t,i}$ ”			
c_{obs}	–	0.05	0.05
$\sigma_{k,s}$	–	0.1	0.2
σ_z	–	0.3	0.3

For each individual in each of the simulation scenarios, sex was sampled from a Bernoulli distribution with mean calculated from the observed sex of individuals in the toothfish data set. The age at first capture of each individual (t_1) was sampled from a log-normal distribution with mean and variance estimated from the observed initial length of individuals in the toothfish data set. The time at liberty (t_2) was sampled from an exponential distribution with shape parameter estimated from the observed time at liberty of individuals in the toothfish data set. The age at recapture ($t_1 + t_2$) was calculated as the age at first capture (t_1) plus the time at liberty (t_2).

We conducted 200 simulation replicates for each of the 8 simulation scenarios. To each replicate, we fitted four different versions of the model. These models included: no random-effects, random-effects for the persistent differences in upkeep costs for each sex ($k_{i,s}$ only), transient variation in growth ($z_{\Delta t,i}$ only), and random-effects representing both persistent and transient variation in growth ($k_{i,s}$ and $z_{\Delta t,i}$). This resulted in 32 different simulation/estimation model combinations, each of which were fitted 200 times (i.e., 6400 model fits).

Instead of reporting average energy acquisition rate (γ_s) we present the derived median asymptotic length ($\mu_{L_{\infty,s}}$) which is calculated using Eq. (6).

2.3. Case study application

Antarctic toothfish are large Nototheniids native to the Southern Ocean. They can grow to be more than 2 m in length, weighing over 100 kg, and can live for up to 50 years of age. The exploratory toothfish fishery in the Ross Sea region began in 1997 and is managed by The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Since then the fishery has increased to about 3000 tonnes per year. Fishing is restricted to the austral summer months (December usually until March), once the ice shelf recedes allowing vessels access to the region. The Antarctic toothfish tagging programme was initiated in the 2001 fishing season by New Zealand vessels involved in the fishery. In 2004, toothfish tagging

was made compulsory for all vessels participating in the fishery. Currently toothfish are required to be double tagged at a rate of one fish per tonne landed. The tagging programme records information on the date, depth, location, sex, and size of each tagged/recaptured fish. A small subset of the recaptured fish are aged by reading their otolith. The otoliths are assumed to be aged without error as the ageing error is known to be minimal for this species (Dunn et al., 2006).

We identified those fish that had been tagged, recaptured and aged upon recapture. This yielded 315 individuals of which 166 were female and 149 male. All individuals were originally tagged between 2001 and 2008, and were subsequently recaptured between 2002 and 2013. These data allowed us to identify the observed length (cm) at first capture $L_{obs}(t_1)$ and recapture $L_{obs}(t_1 + t_2)$. The time at liberty (t_2) and the measured age of the fish at recapture ($t_1 + t_2$) was used to calculate the age of the fish at tagging (t_1). We fit four different versions of the model to these data, these included: no random-effects, random-effects for the persistent differences in upkeep costs for each sex ($k_{i,s}$ only), transient variation in growth ($z_{\Delta t,i}$ only), and random-effects representing both persistent and transient variation in growth ($k_{i,s}$ and $z_{\Delta t,i}$).

Similar to the simulations, length at birth ($L_{0,s}$), average upkeep costs ($\mu_{k,s}$), the magnitude of persistent variation in growth ($\sigma_{k,s}$) and average energy acquisition rates (γ_s) were all assumed to be sex-specific in the application of these models. The magnitude of transient variation in growth (σ_z) and the magnitude of error when measuring length (c_{obs}) were assumed to be the same for males and females.

Preliminary exploration suggested that ψ was often not estimable for our data set as most models attempting to estimate this parameter did not converge. However, when models did converge, estimates of the parameter were close to zero so we proceed by fixing $\psi = 0$. We do not explore the behavior of different values of ψ further, but recommend it as a topic for future research. Seasonal effects could not be explored because all tagging and recaptures are observed during a few months (December–March and a few in May) and hence seasonal variation is included in estimates of transient variation in growth rates.

3. Results

3.1. Simulation

Estimates of median upkeep costs ($\mu_{k,s}$) and median asymptotic maximum length ($\mu_{L_{\infty,s}}$) are unbiased in most scenarios of both simulation experiments (different data-generating models: Fig. 1, power analysis: Fig. 2, panel A–H). However, the model performs poorly when data are simulated with persistent variation in growth ($k_{i,s}$ only or $k_{i,s}$ and $z_{\Delta t,i}$) but the estimation model only considers transient variation in growth ($z_{\Delta t,i}$), even with high sample sizes (i.e., $n = 500$ individuals; Fig. 2, panel D and H). In the power-analysis experiment, estimates of median upkeep costs ($\mu_{k,s}$) and median asymptotic maximum length ($\mu_{L_{\infty,s}}$) become more precise (i.e., the distribution of estimates around the true value gets tighter) as the sample size (n) is increased from 50 to 500 individuals (Fig. 2, panel A–H).

The size at birth ($L_{0,s}$) is also unbiased in both simulation experiments (Figs. 1 and 2, panel I–L). But again, the model performs poorly given data simulated with persistent variation in growth ($k_{i,s}$ only or $k_{i,s}$ and $z_{\Delta t,i}$) but when only estimating transient variation in growth ($z_{\Delta t,i}$; Fig. 1, panel J and L). Estimates of this parameter are imprecise (i.e., a SD of 15.0 and 21.0, for females and males respectively, when estimated with both transient and persistent variation in growth rates) given low sample sizes (i.e., $n = 50$ individuals; Fig. 2, panel I). The precision improves markedly with increasing

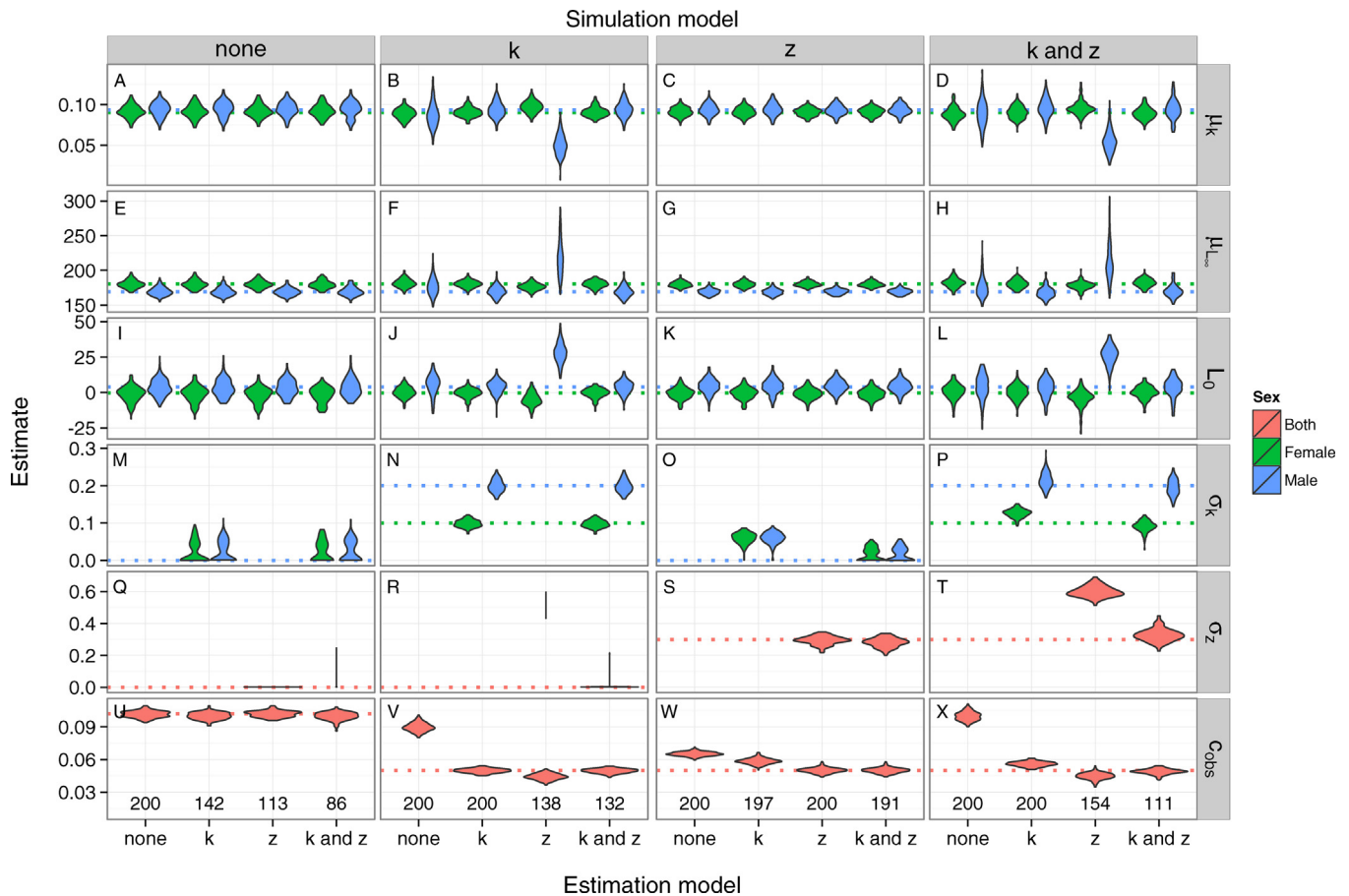


Fig. 1. Violin plots of the estimated value of each parameter by sex, using each of the four estimation models (x-axis), for each of the four simulation models (above top panels). The parameters estimated include the median upkeep cost ($\mu_{k,s}$, years⁻¹), median asymptotic length ($\mu_{L_{\infty,s}}$, cm), length at birth ($L_{0,s}$, cm), magnitude of persistent variation among individuals ($\sigma_{k,s}$), magnitude of transient variation among individuals (σ_z), and coefficient of variation of observation error (c_{obs}). The dotted horizontal lines show the true simulated values of each parameter. The number of fits that are positive definite Hessian are given in the bottom panel. Each panel is labelled alphabetically and individual panels are referred to in the text.

sample size (Fig. 2, panel J–L), and has an SD of 3.8 and 4.5, for females and males respectively, for large sample sizes when estimating both persistent and transient variation ($n = 500$ individuals; Fig. 2, panel L).

The magnitude of persistent variation among individuals ($\sigma_{k,s}$) was approximately unbiased when a model that estimates persistent growth variation was applied to data from a model that simulates persistent growth variation (Fig. 1, panel N and P). However, when attempting to estimate this parameter from a model that does not simulate persistent growth variation, this parameter was often overestimated (Fig. 1, panel M and O). In the power-analysis simulation experiment, this parameter was approximately unbiased for all sample sizes, and relatively precise at sample sizes above $n = 100$ (Fig. 2, panel O and P), with a small proportion of parameter estimates hitting the lower bound when sample sizes were small (Fig. 2, panel M and N).

The magnitude of transient variation (σ_z) was generally estimated to approach zero when a model that estimates transient growth variation was fitted to simulated data without transient variation (Fig. 1, panel Q and R). Estimates of the magnitude of transient variation were biased high when a model with transient random-effects only was fitted to data that was simulated with persistent variation in growth (Figs. 1 and 2, panel R and T). The bias in these scenarios occurred because the model was attempting to account for persistent variation in individual growth via the transient-variation component.

Finally, estimates of the c.v. of observation error (c_{obs}) were biased high, in both simulation experiments, when a model with no random-effects was fitted to a model with either persistent or transient variation in growth (or both; Figs. 1 and 2, panel V–X), because persistent and transient variation were confounded with observation error in these scenarios. However, the c.v. of observation error was well estimated when an estimation model was fitted to its corresponding simulated data set (e.g., data was simulated with transient variation in growth and the model that estimates transient random-effects was fitted to these data) or in any scenario if the model that estimates both persistent and transient variation in growth was used (Figs. 1 and 2, panel U–X).

Not all fits to simulated data had a positive definite Hessian, signifying that some combinations of simulation replicate and estimation model had parameters that were either (1) not converged or (2) not uniquely identifiable given the information in that simulated data set. When the estimation model included no random-effects, or random-effects for upkeep costs ($k_{i,s}$) only, almost all model fits were positive definite. Fewer simulation replicates were positive definite when the model incorporated transient individual random effects ($z_{\Delta i,i}$), particularly at lower sample sizes (see Fig. 2). However, we note that most models were positive definite for sample sizes above 250 individuals, and that non-positive definite models can be used as an indication that the model is likely to be overfitted relative to the available data.

In summary, the simulation study shows that: (1) when the structure of the estimation model matches that of the simulated

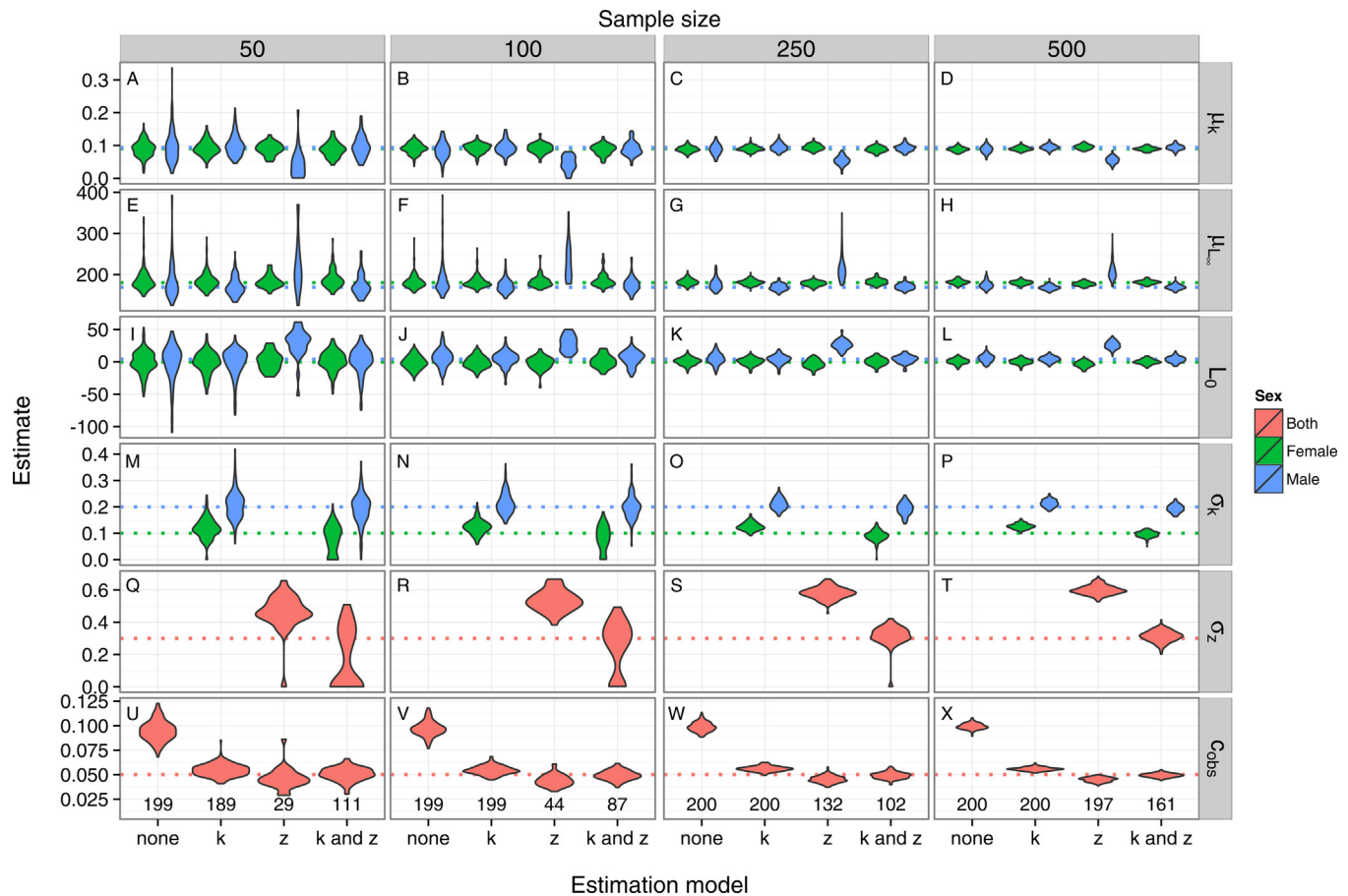


Fig. 2. Violin plots of the estimated value of each parameter by sex, using each of the four estimation models (x-axis), for each of the four sample size scenarios (50, 100, 250 and 500 individuals, above top panels). The parameters estimated include the median upkeep cost ($\mu_{k,s}$, years⁻¹), median asymptotic length ($\mu_{L_{\infty,s}}$, cm), length at birth ($L_{0,s}$, cm), magnitude of persistent variation among individuals ($\sigma_{k,s}$), magnitude of transient variation among individuals (σ_z), and coefficient of variation of observation error (c_{obs}). The dotted horizontal lines show the true simulated values of each parameter. The number of fits that are positive definite Hessian are given in the bottom panel. Each panel is labelled alphabetically and individual panels are referred to in the text.

data, the model can accurately estimate the growth parameters; (2) an estimation model that accounts for persistent ($k_{i,s}$) and transient ($z_{\Delta t,i}$) variation in growth can provide unbiased growth estimates even if the data is not simulated using a model that includes persistent or transient variation, while accounting for only persistent or transient variation (or neither) in the estimation model could result in biased growth estimates; and (3) only small gains in the precision of parameter estimates are made by increasing the case study sample further than $n = 250$.

3.2. Case study application

When applied to data for Antarctic toothfish in Ross Sea, the model without random-effects looks much like a standard von Bertalanffy growth curve for both females and males (Fig. 3). The residual fit of this model is poor, given that many individuals have a positive/negative residual at both tagging and resighting, and therefore residuals are correlated for a given individual (Fig. 4). The model without persistent or transient growth variation was the least parsimonious model of the four according to the Akaike information criterion (AIC; Akaike, 1998; Table 3).

Compared to Dunn et al. (2006) this models estimate of the magnitude of residual variation (c_{obs}) was very similar at 0.111 (compared to 0.102). However, this model estimated a larger size at birth ($L_{0,s}$) and larger median asymptotic maximum length ($\mu_{L_{\infty,s}}$). Using Eq. (7), the length at birth ($L_{0,s}$) from Dunn et al. (2006) is -0.34 cm and 3.98 cm for females and males, respectively. Here

the length at birth ($L_{0,s}$) was estimated to be 46.51 cm and 51.54 cm (Table 2). Using Eq. (6), the median asymptotic length ($\mu_{L_{\infty,s}}$) was 216 cm and 177 cm for females and males, respectively (compared with 180.20 cm and 169.07 cm in Dunn et al., 2006). Differences in the estimates of length at birth ($L_{0,s}$) and median asymptotic length ($\mu_{L_{\infty,s}}$) compared to Dunn et al. (2006) are likely due to differences in the sample size of small/young and large/old individuals between the two studies, rather than any difference in methodology. Our study included 315 individuals from age 3 to 30, with few individuals below age 5 or above age 20. Dunn et al. (2006), by contrast, included 4569 individuals from age 3 to 48 in their study, and had a greater sample size of individuals below age 5 and above age 20. Therefore, we conclude that their study is more credible for estimating the size of young and old individuals. Obviously our estimates of median asymptotic maximum length ($\mu_{L_{\infty,s}}$) are not actually representing length at age 0 (which is likely to be close to zero), instead our model is just extrapolating based on growth patterns for older individuals. We suggest that estimates of length at birth ($L_{0,s}$) and median asymptotic length ($\mu_{L_{\infty,s}}$) in our study could be improved by an increased availability of tagging data for young and old individuals. Despite this, our model is likely to provide good estimates of length across the range of ages available and has the ability to provide estimates of persistent or transient variation in growth.

The most parsimonious model (which has AIC 160 lower than the model without random effects; Table 3), included transient individual variation in growth rates ($z_{\Delta t,i}$, Fig. 3). We note that

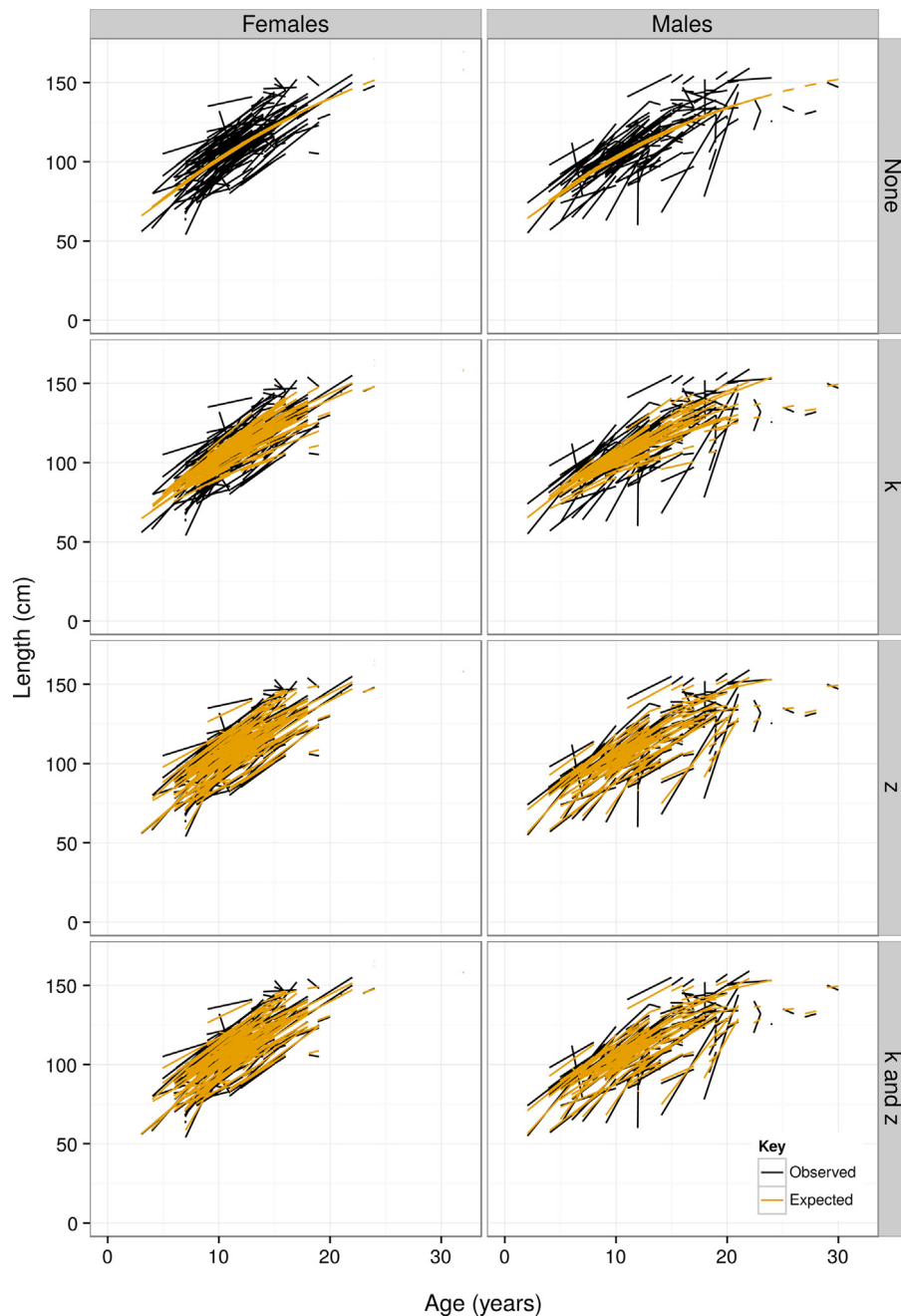


Fig. 3. Observed and expected length (cm) at age (years) for individual female and male Antarctic toothfish using the model with no random-effects, persistent variation (estimating variation in $k_{i,s}$ only), transient variation in growth (estimating variation in $z_{\Delta t,i}$ only), and both persistent and transient variation (estimating variation in $k_{i,s}$ and $z_{\Delta t,i}$).

the simulation experiment identified a lack of performance of this model in estimating the correct parameter values when data are simulated from a model with persistent growth variation. However, the model that included both persistent and transient variation in individual growth rates ($k_{s,i}$ and also $z_{\Delta t,i}$) resulted in no decrease in marginal likelihood, and was deemed to be less parsimonious by AIC due to its inclusion of one additional fixed effect (Table 3). Furthermore, the maximum likelihood estimate of the magnitude of persistent variation ($\sigma_{k,s}$) approached zero for both sexes, indicating little evidence of persistent variation in growth within the Antarctic toothfish data set. For these reasons, and because the models that include transient individual variation in growth rates ($z_{\Delta t,i}$) and persistent and transient variation in growth rates ($k_{i,s}$ and $z_{\Delta t,i}$) produce similar results (Fig. 3), we suggest that the model

that includes transient individual variation in growth rates ($z_{\Delta t,i}$ only) is the best choice for these data.

In this model, the standard deviation in log-space of transient variation (σ_z) was 0.632, representing a 70% coefficient of variation in annual (transient) growth rates for each individual in each week. This model produced a tighter fit than the model that did not consider persistent or transient variation in growth rates (Fig. 3). The distribution of residuals for each individual at tagging and recapture are approximately uncorrelated, with the exception of a few males that are either smaller than expected at tagging or larger than expected at resighting (or vice versa, Fig. 5). Values for most estimated parameters were similar to those estimated in the model without the inclusion of any random-effects, however, the estimated c.v. of residual errors is lower (AIC-selected

Table 3
Estimated parameter values in each of the four case study models by sex (s). ΔAIC is the difference in Akaike information criterion between the current model and the most parsimonious model. Values marked with an asterisks (*) are hitting the lower bound.

Model	ΔAIC	Parameter	Units	Female	Male
No variation	160	$L_{0,s}$	cm	46.51	51.45
		k_s	years ⁻¹	0.040	0.054
		γ_s	years ⁻¹	8.669	9.534
		c_{obs}	–	0.111	0.111
Variation in $k_{i,s}$	92	$L_{0,s}$	cm	45.70	52.11
		$\mu_{k,s}$	years ⁻¹	0.041	0.046
		γ_s	years ⁻¹	8.864	8.801
		c_{obs}	–	0.083	0.083
		$\sigma_{k,s}$	years ⁻¹	0.240	0.217
Variation in $z_{\Delta t,i}$	0	$L_{0,s}$	cm	34.66	45.82
		k_s	years ⁻¹	0.062	0.054
		γ_s	years ⁻¹	11.371	9.896
		c_{obs}	–	0.048	0.048
		σ_z	cm	0.632	0.632
Variation in $k_{i,s}$ and $z_{\Delta t,i}$	4	$L_{0,s}$	cm	34.66	45.82
		$\mu_{k,s}$	years ⁻¹	0.062	0.054
		γ_s	years ⁻¹	11.371	9.896
		c_{obs}	–	0.048	0.048
		$\sigma_{k,s}$	years ⁻¹	0.001*	0.001
		σ_z	cm	0.632	0.632

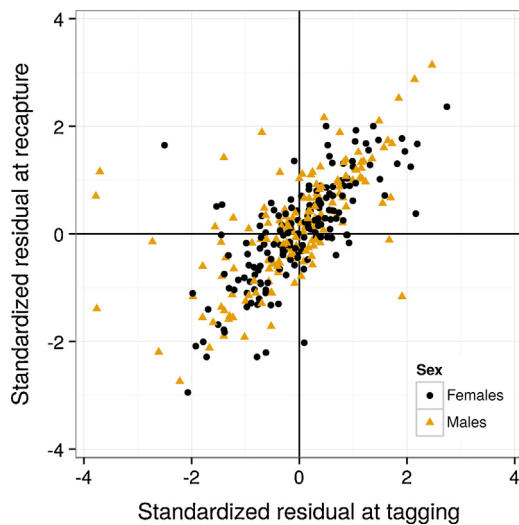


Fig. 4. Standardized residual in length at tagging vs. the standardized residual in length at recapture (cm) for individual female and male Antarctic toothfish using the model with no random-effects. The standardized residual is calculated as $L_{obs}(t) - L(t) / SD(L_{obs}(t) - L(t))$ where SD is the standard deviation.

model: $c_{obs} = 0.05$ vs. model without random effects: $c_{obs} = 0.102$) as over half of the variability is apportioned into the time-varying individual variation (σ_z ; Table 3).

4. Discussion

In this study, we used a simulation experiment and a case study application for Antarctic toothfish to demonstrate that it is feasible to simultaneously estimate persistent and transient variation in growth among individuals, as well as differences in growth rate between females and males and residual (measurement error) variation in a natural population of a marine fish species. Early studies incorporated variability in growth via individual variation in growth parameters (Sainsbury, 1980) or both time-dependent and time-independent variation in growth increments (Francis, 1988). Recent studies have developed mixed-effect models for estimating variation in growth rates over time and/or among individuals in wild or experimental settings involving fish (Shelton et al., 2013;

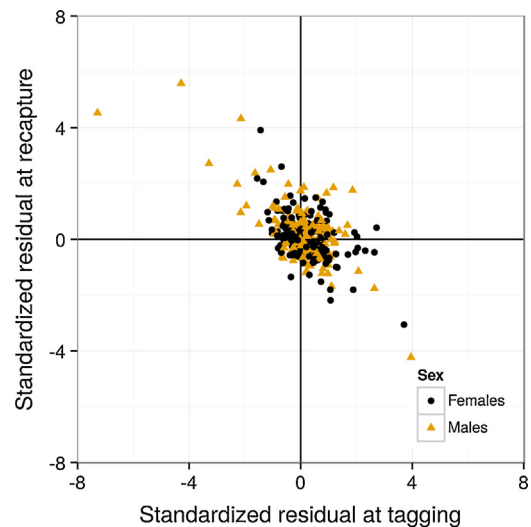


Fig. 5. Standardized residual in length at tagging vs. the standardized residual in length at recapture (cm) for individual female and male Antarctic toothfish using the model with transient variation in growth. The standardized residual is calculated as $L_{obs}(t) - L(t) / SD(L_{obs}(t) - L(t))$ where SD is the standard deviation.

Snover et al., 2005; Stawitz et al., 2015; Thorson and Minte-Vera, 2016; Vincenzi et al., 2014). Variation in growth rates is also an active area of research and method development in other ecological taxa (e.g., Brooks et al., 2013). However, our study is the first to our knowledge to estimate persistent and transient variation in growth in a wild marine population. Our case study application suggests that transient variation among individuals accounts for up to half of the total variability in Antarctic toothfish.

By estimating persistent and transient variation among individuals and between sexes, we have largely eliminated the correlations in residual size between tagging and recapture, as was seen in the toothfish data set for the model without random effects. However, we have neglected two obvious types of variation in growth rates: persistent variation over space, and synchronous variation that is similar among individuals (i.e., temporal variation, among seasons or years). Populations may experience synchronous variation in growth rates for several reasons. For example, annual variation in water temperature may drive changes in metabolic

costs as well as food availability in upwelling systems such as the California Current (Black et al., 2010), and this may cause all individuals to have elevated or depressed growth rates in a given year. Recent meta-analytic work supports the hypothesis that time-variation in average growth rates is the rule rather than the exception for marine populations (Thorson and Minte-Vera, 2016). Similarly, many studies have illustrated persistent spatial differences in growth rates (Gertseva et al., 2010), e.g., where populations often have a smaller maximum size in warmer waters. Previous research has demonstrated the prevalence of spatial variation in growth (Gertseva et al., 2010) and condition (Thorson, 2015). The modelling framework we present here could easily be modified to include spatial variation in growth rates, either among spatial strata or using geostatistical techniques (Shelton et al., 2014; Thorson et al., 2015), but in this study we have chosen instead to focus on testing the individual, temporal, and sex-specific variation that we presented here. We hypothesize that including spatial variation would decrease the magnitude of among-individual variation in growth rates, because spatial variation would explain some portion of individual-level variation.

We note that our model (and results for Antarctic toothfish in the Ross Sea) does not account for the effects of fish handling and tagging on growth rates. Growth rates for untagged individuals may be higher because tagging is likely to cause physiological stress that depresses activity and metabolic levels (Dubula et al., 2005; Santos and Groeneveld, 2015; Xiao, 1994). Future studies could estimate the impact of tagging on growth rates by jointly analyzing CMR and other fishery data types (termed “integrated growth models”; Eveson et al., 2004). In particular, the length-frequency of fishery and survey catches and the direct ageing of hard parts from catches provide a separate source of information regarding size at age. These latter two sources of information do not generally provide information to discriminate between persistent and transient variation in growth rates (because each involves measuring size only once for each individual). However, both sources can provide complementary information regarding average growth rates for untagged individuals. We therefore believe that estimating persistent and transient variation in growth rates within integrated growth models is an important topic for future research.

Information regarding the magnitude of persistent and transient variation in growth is important for at least three reasons. First, stock assessment models and fisheries management strategies are routinely evaluated using simulation experiments (termed “management strategy evaluation”; Sainsbury et al., 2000). However, simulation experiments depend upon having information regarding plausible states-of-nature, which are used to simulate available data (Punt, 2008). Models estimating time-variation in growth can be used to simulate more plausible data for use in testing assessment methods. Second, estimating the magnitude of persistent variation in growth will lead to improved methods for approximating growth in population models. In particular, persistent individual variation in growth has recently been approximated by tracking individual platoons of fishes having the same age but different average growth rates (Taylor and Methot, 2013). Tracking abundance by platoon then allows stock assessment models to account for the impact of size-selective fishing on average growth rates. In particular, improved accounting for growth is likely to be important for models that are highly dependent upon growth information, e.g., length-based spawning potential ratio assessments (Hordyk et al., 2015). Third, consistent with the results of our simulation study, previous research has indicated that growth estimates can be biased when estimated via models that do not account for variation in growth (Sainsbury, 1980), and that these biases can in turn result in biased estimates of stock status and productivity (Punt et al., 2016). We therefore hypothesize that improved treatment of transient and persistent individual variation in growth will

improve estimates of growth rates obtained from CMR data sets, and that this improvement may result in improved estimates of fishery productivity.

5. Conclusions

In this study, we have estimated the magnitude of persistent and transient variation in growth rates among individuals in a wild marine population of Antarctic toothfish in the Ross Sea during 2001–2013, in addition to differences in average growth rates between females and males. Model selection suggests that transient variation is more significant than persistent variation among individuals during these years. Estimating transient variation decreased the coefficient of variation of residual (measurement error) variation by nearly half. Our simulation study corroborates that all models provide parameter estimates that are approximately unbiased and reasonably precise given sample sizes similar to those available here. Finally, we provide an R package *TagGrowth*, containing code for applying our estimation model to other data sets. We encourage future research comparing the magnitude of persistent and transient variation in growth among marine populations in different taxa and environments.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2015.08.016>.

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