**Tag-recapture Antarctic toothfish random effects environment**

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**Abstract**

**Keywords:** Antarctic toothfish; time-varying growth; random effect; von Bertalanffy growth function

## Introduction

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 cause changes in the risk of predation. Finally, environmental conditions modulate 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. Similarly, changes in survival rates (via fishery harvest) may favor earlier maturation, thus affecting the relative allocation of energy between growth and reproduction.

Many recent studies of captive or wild populations have demonstrated persistent differences in behavioral or phenotypic traits among individuals (termed differences in “personality”). Persistent differences in activity level or tolerance of predation risk (i.e., when foraging in high vs. low-quality habitat) will likely lead to persistent differences in growth rates. Variation in growth rates has been discussed for over 100 years for fish populations. For example, persistent differences in growth rate, combined with size-selective harvest, will result in older individuals being composed primarily of slow-growing individuals (termed “Rosa Lee’s Phenomenon”). Failure to account for persistent differences in growth rate can therefore lead to biased estimation of average growth rates in wild populations, and population dynamics models are increasingly developed to account for these effects (Taylor and Methot 2013).

In addition to persistent differences in growth rate among individuals, populations may experience synchronous variation in growth rates in a given year. 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 works has supported the hypothesis that time-variation in average growth rates is the rule rather than the exception for marine populations (Thorson and Minte-Vera In press). 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.

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. Spatial variation (i.e., some areas have different size at age on average than others)
3. Temporal variation (i.e., all individuals having elevated or depressed growth rates in a given year)
4. Residual variation (i.e., individuals will have spurts and drops in growth rates).

Mixed-effects models are generally used to decompose variance in a data set into multiple sources of variability (Thorson and Minto In press). Mixed-effects models accomplish this by estimating true size at age as a latent variability, which is integrated across during estimation of growth parameters. 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 (Larsen et al. 2001, Gelman 2005).

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. 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 imapct of persistent or residual variation on estimation of growth patterns using CMR data for wild marine populations (Sainsbury 1980, Francis 1988). However, few studies have explicitly modeled multiple sources of variability in growth rates. One exception is Shelton et al. (2013), which modeled persistent, temporal, and residual variation in growth rates in the analysis of data from a growth experiment for steelhead trout. In this study, we additionally incorporate sex-specific differences and spatial variation in growth rates, and implement the model using maximum marginal likelihood estimation. The code is distributed as a publicly available package in the R statistical environment, and is illustrated using CMR data for Antarctic toothfish. Using these data, we show that …. [1-2 sentence summary of most important result for toothfish].

**Methods**

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 In press). We start with the specialized von Bertalanffy growth function:

where *dL/dt* is change in length as a function of time, *a* scales with energy acquisition, and *b* represents metabolic upkeep costs. Individuals that are more highly active may obtain more food (increased *a*) and simultaneously have greater upkeep costs (increased *b*). Following Shelton et al. (2013), we include this correlation via the following equation:

(2)

where *γ* and *Ψ* approximate the allometric scaling of energy costs and acquisition. Integration then yields:

where

where *Δt* is the number of time-periods elapsed between length intervals, and where the Brody growth coefficient (as in the conventional von Bertalanffy growth function). The asymptotic length can be found by setting Eqn. 1 equal to zero, substituting in Eqn. 2, and rearranging:

Penalized likelihood, the prior on the Linf par acts as a penalty function.

Set at mu=and sig= (Dunn et al. 2006).

Readers are referred to Shelton et al. (2013) for an expanded model that incorporates variability in *γ* over time, although we retain the assumption that *b* varies among individuals (and hence has subscript *i*), where it follows a normal distribution (truncated at zero) with estimated mean and variance parameters.

Following previous notation, parameters are estimated by integrating across all random effects ***b***, while noting that Eq. 3 also requires estimation of *Li(t0)*, i.e., the length upon first observation for each individual.

We implement this model using the *Template Model Builder* (*TMB*) software called from *R* using the *TMB* package and provide the code as an example of how to call *TMB* from *R* (Appendix A). We fit the model to data collected in the Antarctic toothfish (*Dissostichus mawsoni*) tagging programme wherein each individual is uniquely tagged and aged at recapture.

So

Sex-specific gamma could not be estimated (see v7).

Table 1 – List of model runs.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Model run | Time-step | Linf penalty | L0 penalty | tvi | Y devs | Area devs |
|  | Daily |  |  |  |  |  |
| V9 | Weekly | x |  | x |  |  |
|  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |

## Simulation

A simulation study was done to validate the model.

## Discussion

Mention how when the model was fit to annual rather than daily growth increments that the estimated parameters resulted in biased high growth schedules.

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**Appendix A – Code for calling *TMB* from within *R***

Table 2 – List and definition of symbols used in the text and equations.

|  |  |  |  |
| --- | --- | --- | --- |
| Parameter name | Symbol | Units | Dimensions |
| Individual |  |  |  |
| Time |  | Days |  |
| Sex |  |  | 2 |
| Area |  |  |  |
| Length |  | cm |  |
| The hypothetical length at |  | cm |  |
|  |  | Days |  |
| Anabolic rate |  |  |  |
| Catabolic rate |  |  |  |
|  |  |  | 1 |
|  |  |  | 1 |
| Time variation |  |  |  |
| Asymptotic maximum length |  | cm |  |
| Brody growth coefficient |  |  |  |
| The hypothetical time at which |  | Days |  |
| Observation error standard deviation |  |  | 1 |
| Catabolic rate standard deviation |  |  |  |
|  |  |  | 1 |
|  |  |  | 1 |
|  |  |  | 1 |