Fisheries Research 180 (2016) 67–76

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

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

D'Arcy N. Webber[a,*], James T. Thorson[b]

[a] Quantifish, 1 Saint Michaels Crescent, Kelburn, Wellington 6012, New Zealand
[b] Fisheries Resource Assessment and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd. East, Seattle, WA 98112, United States

ARTICLE INFO

Article history:
Received 28 February 2015
Received in revised form 13 August 2015
Accepted 13 August 2015
Available online 28 August 2015

Keywords:
Antarctic toothfish
Time-varying growth
Random effect
von Bertalanffy growth
Individual growth variation
Persistent growth variation
Transient growth variation

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.

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,

* Corresponding author.
E-mail address: darcy@quantifish.co.nz (D.N. Webber).

http://dx.doi.org/10.1016/j.fishres.2015.08.016
0165-7836/

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:

$$\frac{dL}{dt} = a - kL \tag{1}$$

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:

$$k_i = \mu_k \exp\left(\epsilon_i^k\right) \tag{2}$$

where $\epsilon_i^k \sim N\left(0, \sigma_k^2\right)$, 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:

$$a_i = \gamma k_i^{\psi} \tag{3}$$

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:

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

where

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