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Effects of age-based movement on the estimation of growth assuming random-at-age or random-at-length data

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Running headline: AGE-BASED MOVEMENT AND ESTIMATION OF GROWTH

Simulation methods were used to generate paired data from a simulated population that included the age-based process of movement and the length-based process of gear selection. The age-based process caused bias in the estimates of growth parameters assuming random at length, even when relatively few age classes were affected. Methods that assumed random at age were biased by the subsequent inclusion of the length-based process of gear selection. Additional knowledge of the age structure of the sampled area is needed to ensure an unbiased estimate of the growth parameters when using the length-conditional approach in the presence of age-based movement. Estimates of the variability in the length-at-age relationship were better estimated with the length-conditional than the traditional method even when the assumptions of random at length were violated. Inclusion of paired observations of length and associated age inside the population dynamics model may be the most appropriate way of estimating growth.

Key words: age-based growth; von Bertalanffy; gear selection; length-based growth; simulation.

INTRODUCTION

Age determination and estimation of growth are fundamental components of fisheries biology (Ricker, 1969; Beamish & McFarlane, 1983). The growth form can be described by growth models whose parameters are usually estimated from paired observations of fish length and an associated age. In most studies fish length is a measured property while the age is estimated from hard parts (*e.g.* otolith, scale and spine). The most commonly used representation of fish growth is the von Bertalanffy growth model (von Bertalanffy, 1938). Its widespread use includes extensions for auto-correlated samples (Jones, 2000) and studies lacking explicit age information (Hart & Chute, 2009). When independent paired age–length observations are available, however, the statistical methods used to estimate growth usually make one of two assumptions about the data (Francis, 2016). The most common assumption is random at age, referred to as the traditional method, where each paired observation is asserted to be representative of the distribution of lengths for a given age. Less common is the assumption of random at length, referred to as the length-conditional method, where each paired sample is asserted to be representative of the distributions of ages for a given length.

The most familiar method (traditional) of estimating growth model parameters assumes length observations are random at age. Traditional estimation compares the predicted length at age from the model with the observed lengths at age from the paired observations. This traditional method is relatively straightforward to perform and has been used in the overwhelming majority of growth studies (Ross, 1988; Piner & Jones, 2004).

A length-conditional method estimates the growth parameters assuming random-at-length observations (Hoyle & Maunder, 2006; Taylor & Methot, 2013; Piner *et al*., 2016). The length-conditional method compares the observed distribution of ages for a given length to the distribution predicted by the growth model. The model predictions of the expected age distribution for a given length are partially determined by the population age structure that was sampled. The advantage of the length-conditional method is the separation of the process error (growth variability) from the observation error (measurement, ageing and sampling error). The separate treatment of error may facilitate a better estimate of the variability in the length-at-age relationship (Piner *et al*., 2016, Xu *et al*., 2016), which is often an overlooked, but important component of the growth form. Because the length-conditional method relies on an estimate of the population age structure, growth parameter estimation with this method has largely been confined to inside the population dynamics model (Hoyle & Maunder, 2006; Methot & Wetzel, 2013). Recently, the length-conditional method was extended by using an equilibrium approximation of the age structure allowing estimation outside the population dynamics model (approximate length-conditional method, Piner *et al*., 2016).

Knowledge of the population life history and the sampling design determines which assumption (if either) is the most appropriate. Because the age is usually not determined until after sample collection, growth studies will often report random sampling as validating the assumption of random at age. Random sampling of the population where each individual (age–length pair) has an equal probability of being sampled ensures the population length distribution for a given age is randomly sampled. Paired samples that are taken from the population with an intervening length-based process, such as length-stratified sampling or random dockside sampling from length-selective gears, can invalidate this assumption (Piner *et al*. 2016). In contrast, the assumptions behind the length-conditional method can be met using both random sampling of the population and length-stratified designs or equivalently sampling from length-selective gears. If samples were collected with an intervening age-based process (*e.g.* movement), however, the assumption of random at length could be invalidated. Understanding which processes are influencing sample collection needs to be considered when evaluating what assumptions, if any are appropriate for the paired data.

A considerable body of research has demonstrated that growth estimation methods assuming random at age can show significant bias when that assumption is violated (Ricker, 1969; Taylor *et al*., 2005; Schueller *et al*., 2014; Piner *et al*., 2016). There is comparatively little known about the effects of violating the assumption of random at length because of the greater data demands and the relative newness of the length-conditional method. This work attempts to address this shortcoming using simulation methods to understand the effects on growth estimation from paired age-length samples taken with an intervening age-based process or a combination of age and length-based processes. The study focuses on the consequences to the length-conditional (random-at-length) estimation method by comparing with true estimates and to those from the traditional method (random-at-age) as well.

MATERIALS AND METHODS

This study simulated spatially explicit (two areas) population dynamics to examine the effects on growth parameters estimation from the sampling of age-length pairs with an intervening age-based process (age-based movement) and subsequently the age-based process along with the length-based process of gear selection. The age-based movement results in each area containing different components of the total population age structure. Three growth estimation methods were evaluated: the first assumed random at age (traditional), the second assumed random at length without knowledge of the age-based process (incorrect length-conditional) and the third assumed random at length with knowledge of the age-based process (correct length-conditional). The methods are explained starting with simulation of synthetic populations, sampling from simulated populations, estimation of growth models and finally comparison of the parameter estimates (Fig. 1).

SIMULATION METHODS

Stock synthesis (SS; Methot & Wetzel, 2013) was used as the simulation model to create synthetic populations. Stock synthesis is a forward simulating integrated population dynamics model that keeps track of both numbers at age, numbers at length as well as age at length by user defined spatial areas. SS is normally used to fit to data to estimate the population dynamics; this study, however, used the model structure to generate spatial population dynamics and create paired age–length data.

Parameters controlling the systematic processes governing the spatial population dynamics were stochastically generated (Table I) and used to simulate 10 000 synthetic populations with known length-at-age relationships. Two life histories were simulated separately, a short-lived fast growing and a long-lived slow growing population. Two spatial areas with separate dynamics were linked by one-way, age-based movement. All age 0 years recruits settled in the juvenile area (area 1) and subsequently moved to the adult area (area 2) at an increasing rate with age [Table I and Fig. 2(a)].

Population dynamics were simulated for 63 years to allow for multiple generations to minimize the effect of assumptions about the initial conditions. Simulations of population dynamics and sampling included a fishery operating in each area with exploitation levels associated with the stochastic choice of the natural mortality coefficient (Table I). Fishery removals included a length-based asymptotic gear selectivity pattern [Fig. 2(b)]. In addition to the fishery in each area, a hypothetical survey operation (with minimal catch) using a non-selective gear (all ages and lengths fully selected) was also simulated in each area.

SAMPLE SELECTION

For each simulated population, 10 000 paired lengths and associated ages were randomly sampled in the terminal year from both the juvenile (area 1) and adult (area 2) areas. Fish from these respective areas were sampled either from the simulated fishery or the simulated survey operation. Samples taken from the juvenile area contained mostly young fish and those from the adult area a mixture of juvenile and adult fish. Samples taken from the survey in each area were influenced only by the age-based process of movement because the gear was non selective. Samples taken from the fishery in each area included a length-based process of gear selection in addition to the age-based movement. For each combination of life history (short or long-lived), area (mostly juvenile or adult) and survey or fishery (age-based or age and length-based process); three growth models were developed: traditional method, incorrect length-conditional using age structure from the entire population and correct length conditional using age structure from the area sampled.

GROWTH MODEL

The growth model used in this study was the von Bertalanffy (VB) growth equation (von Bertalanffy, 1938):

$$L_t = L_{\text{ø}}\left(1 - e^{-K(t-t_0)}\right) + \qquad (1)$$

where L_t is the length of the fish at a specific age (t), L is the theoretical average maximum length, K is the growth coefficient and is the error. Age is expressed in years and t_0 is the hypothetical age when average length is zero.

TRADITIONAL METHOD ASSUMING RANDOM AT AGE

The traditional method of fitting the VB model estimates the parameters of the growth model by minimizing the difference between predicted ($\hat{L}_t$) and observed (L_t) lengths. Each observed length is assumed to be representative of the distribution of length at age and the error (ε) is assumed to be normally distributed with a mean of 0 and a S.D. of C.V.$\hat{L}_t$, which includes both process error (variability in growth) and observation error. Observation error for this study was assumed to be entirely sampling error generated in the parametric bootstrapping procedure and not errors in ageing or measuring fish length. Parameter values ($\hat{\theta} = (L$, K, t_0, C.V.) were solved using maximum likelihood assuming a normal error structure.

LENGTH-CONDITIONAL METHOD ASSUMING RANDOM AT LENGTH

In the length-conditional method, the paired age–length samples were structured as a data matrix of $n_{L,t}$, which is the number of fish sampled at length L and age t. The VB fitting procedure minimizes the difference between the observed and predicted $n_{L,t}$. The details of the method relate to how to measure the difference between the observed and predicted values and how to predict $n_{L,t}$. The distribution of ages for a given length is assumed to be random and therefore should follow a multinomial distribution. The total log-likelihood for $n_{L,t}$ given the growth parameters ($\hat{\theta}$) is proportional to the sum of the product of the data ($n_{L,t}$) and the log of predicted conditional proportion of age given length ($\hat{P}(t|L)$) across lengths and ages:

$$\ln L\left(\hat{\theta}\middle|n\right) \sim \sum_L \sum_a n_{L,t} \ln\left(\hat{P}(t|L)\right) \tag{2}$$

The multinomial likelihood does not directly compare the observed and predicted $n_{L,t}$, but rather requires calculation of the predicted proportion at age in a given length bin, $\hat{P}(t|L)$. The simulated population age structure and parameter values of the growth model [equation. (1)] are used to derive the proportion of fish in the population within each age and length bin combination. First, using conditional probability theory, the predicted proportion at age for a given length is calculated:

$$\hat{P}(t|L) = [\hat{P}(L|t)\hat{P}(t)][\sum_a \hat{P}(L|t)\hat{P}(t)]^{-1} \tag{3}$$

where

$$\hat{P}(a) = x_t\,(\sum_t x_t)^{-1} \tag{4}$$

$$\hat{P}(L|t) = [N(L,\mu_t,\sigma_t^2)][\sum_L N(L,\mu_t,\sigma_t^2)]^{-1} \tag{5}$$

x_t is the population number of fish age (t), $N(L, \mu_t, \sigma_t^2)$ is a normal distribution with mean μ_t and variance σ_t^2 evaluated at L.

In fitting the VB equation using the length-conditional method, the error (ε in Equation (1)) is now the process error, assumed to be normally distributed. The error is the same as in the traditional approach ($\sigma_a =$ C.V.$\hat{L}$) except that observation error, which has been separated, is assumed to be multinomial.

The population age structure used in the length-conditional method was derived from each simulated population in two ways. The first incorrectly used the entire population age structure (incorrect length-conditional) and the second, correctly used the subpopulation age structure from the area where samples were collected (correct length-conditional), thus accounting for the age-based movement.

ANALYSIS

The evaluation compared estimates of the parameters L , K and the C.V. of length-at-age relationship from each method with the true values used in the simulation model, Comparison of parameter estimates was performed using estimates of bias and precision. Relative bias (B) is calculated as:

$$B = (\hat{\theta} - \theta)\theta^{-1} \tag{6}$$

where $\hat{\theta}$ is the estimated quantity and θ is the true quantity (used to generate the data) and bias was expressed as a per cent. Precision of the method was described by the distribution of relative bias for method.

RESULTS

Because of settlement and movement, the simulated populations in the adult area contained different proportions of each age class and the influence of length-based selection for short and long-lived fish (Fig. 2). The adult area contained all age classes except for age 0 years; in contrast the juvenile area, is the inverse of adult area containing all age 0 years fish, but a decreasing proportion of subsequent age classes. Thus, paired age-length samples from the juvenile area were likely not to include the oldest ages for some lengths and the adult area would be missing the youngest ages for those lengths. Because of the similarity in the movement patterns between short and long-lived fish, the adult area contained a larger portion of all age classes of the population all fish for a majority of age classes for the long-lived simulation, but a smaller portion of all age classes in the population for the short-lived example, because fish only lived to be 10 years.

SURVEY SAMPLES (AGE-BASED PROCESS ONLY)

Juvenile area

The incorrect length-conditional method used with survey samples taken from the juvenile area was generally the worst performing method (Fig. 3). Estimates of L and K were biased and imprecise with all estimation methods for long-lived fish. For short-lived fish L and K were biased and imprecise for the incorrect length-conditional approach. The estimates of C.V. were unbiased for the correct and incorrect length-conditional method but biased and imprecise for the traditional method for both life histories.

Adult area

Estimates of growth parameters in the adult area were generally less biased and more precise than those from the juvenile area. The incorrect length-conditional method used with survey samples from the adult area was generally the worst performing method, estimates of L and K were biased and imprecise for both life histories (Fig. 4). The traditional method used with survey samples from the adult area was generally the best performing method, estimates of L and K were unbiased and precise for both life histories. Estimates of L and K were unbiased and generally precise with the correct length-conditional method and long and short-lived fish. The estimates of C.V. were generally unbiased and precise for the correct length-conditional method and traditional method for both life histories but moderately biased and imprecise for the incorrect length-conditional method on short-lived fish.

FISHERY SAMPLES (AGE AND LENGTH-BASED PROCESSES)

Juvenile area

The correct length-conditional method used with fishery samples from the juvenile area was generally the best performing method (Fig. 5). Estimates of L and K, across life histories, were generally the least biased and most precise when using the correct length-conditional approach. For short-lived fish, the incorrect length-conditional was the most biased and imprecise estimator of L and K. For long-lived fish the traditional was the most biased estimator of L and K, however all methods estimates of L and K were imprecise. The estimates of C.V. were generally unbiased and relatively precise for both the correct and incorrect length-conditional method, but moderately biased for the traditional method.

Adult area

Estimates of growth parameters in the adult area were generally less biased and more precise than those from the juvenile area. The correct length-conditional method used with fishery samples from the adult area was the best performing method across both short and long-lived fish (Fig. 6). Estimates of L , K and C.V. across life histories were generally the least biased and most precise when using the correct length-conditional method. The incorrect length-conditional method produced bias and imprecise estimates of L , K and C.V. in short-lived fish. The traditional method was the most biased and imprecise method for long-lived fish.

DISCUSSION

Violations of the assumptions of all methods of estimating growth resulted in biased estimates of growth parameters. The magnitude of the estimated growth parameter bias using each approach will depend how strongly the assumption of the method were violated. Sampling from areas with only part of the population age structure can also cause bias in parameter estimates and that bias may be larger when the portion of the population age structure sampled is small. In the present simulated study, growth parameter estimates from samples in the adult area were generally better than the juvenile area, because a larger portion of each population's age structure were represented in the adult area. Researchers should carefully consider the life history of a species and the sampling methods used when determining the best approach to estimate growth.

Sampling from populations with spatial structure caused by the age-based process of movement can produce bias in the estimation of growth from the length-conditional method assuming random at length. The length-conditional method can only be made robust to the age-based movement by incorporating knowledge about the age structure of the sampled area. Even when a small number of the age classes in the total population are affected by movement (long-lived example), the bias caused by using the incorrect population age structure may still be significant. The length-conditional method, however, largely retained its robustness in the estimation of the variation of the length-at-age relationship even without correctly accounting for the age-based process.

As with the length-conditional method, the traditional method of growth estimation needs additional information to properly account for intervening length-based processes, which was represented in the present study by the length-based selectivity associated with fisheries sampling (Ricker, 1969). Problematic length-based processes include not only gear selectivity (Taylor *et al*., 2005; Schueller *et al*., 2014), but dockside sample selection (Piner *et al*., 2016; Xu *et al*., 2016) and potential spatial patterns due to length-based movements. Less naïve traditional methods have been developed to deal with issues like length-based selectivity (Taylor *et al*., 2005; Schueller *et al*., 2014). In many situations, however, it is likely that there are multiple potential intervening processes, including both age and length-based, which may vary through time. Methods that assume either random at length or random at age may need considerable additional information beyond the paired age-length samples to produce unbiased estimates.

Researchers should carefully consider the life history and sampling methods before choosing a growth estimation method.

Choosing the correct approach to estimate growth is not a trivial decision. The length-at-age relationship, including the process error (variability) is a vital component of many stock assessments, especially those that convert size composition into age composition information. Biased estimates of growth can lead to biased estimates from stock assessment models (Maunder & Piner, 2015). Many current integrated stock assessments models now allow for the use of both random-at-length and random-at-age observations (Hoyle & Maunder, 2006; Methot & Wetzel, 2013). Within the integrated modelling framework, both age and length-based model processes can be incorporated to match the intervening sampling processes.

In practice, many applications of these stock assessment models have estimated a length-based selection pattern to account for contact selectivity and spatial availability, but few have included explicit spatial structure (or alternatively also model age-based selection) to account for spatial age-class availability, which is important to consider under the random-at-length assumption of the length conditional approach. It is essential to understand the nature of the process controlling movement (age or length) to correctly account for spatial effects (Francis, 2016). Although estimating growth parameters as part of an integrated population dynamic model may be the best option, stock assessment authors should consider the assumptions of random at length with these spatial issues in mind.

As with most simulation studies, this work greatly simplified a complex situation and the resulting effects of the simplifications are not always clear. The assumption that the variation in the length-at-age relationship was constant across age and year probably contributed to overstating the reliability of estimates of this parameter. Similarly, the distribution of length at age was not allowed to change due to population or fishing processes. Other simplifications include not considering ageing or measurement error and only evaluating logistic fishery selection and one-directional movement patterns. Evaluating combinations of all these components was deemed too complex for this study and for these reasons mentioned above the results should be interpreted with caution. Given the importance of the length-at-age relationship, more work in this area is warranted and because of the potential complexity it may need to be performed on a case-by-case basis.

Researchers attempting to estimate the length-at-age relationship need to consider if length or age-based processes have potentially biased their samples of paired length–age observations. Previous studies have shown that the traditional method of estimating growth can be improved with a correct accounting of intervening length-based processes (Taylor *et al*., 2005; Schueller *et al*., 2014). This study documented that length-conditional methods can be made robust to intervening age-based processes with additional information about ages affected by the process. In many situations, however, it is likely that there are multiple potential intervening processes, including both age and length-based, which may vary through time. Methods that assume either random at length or random at age may need considerable additional information beyond the paired age-length samples to produce unbiased estimates. Integration of paired age–length data inside a spatially explicit population dynamics model using the length-conditional method may provide the most straightforward and unbiased method for the estimation of growth.

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TABLE I. Characterization of the distributions used to create 10 000 simulated populations. All parameter values (except for recruitment deviations and fishing mortality, *F*) were drawn once from the distribution to produce a single simulated population. Annual recruitment deviations and *F* were drawn from the distribution for each year of the simulation. Values with (L) or (S) are specific to long-lived or short-lived populations, respectively. All other values are common to both life histories

Parameter	Distribution	Mean	Variance (C.V. %)
Recruitment			
Log unfished recruitment ($\ln R_0$) (x10^3 fish)	Fixed	9.00	
Steepness (h)	Normal	0.75	10
Standard deviation for recruitment in log space (σ_R)	Normal	0.60 (L) 0.80 (S)	10
Mortality			
Natural mortality year^{-1} (M)	log-normal	0.15 (L) 0.40 (S)	15
Fishing mortality year^{-1} (F)	Normal	M	20
Growth			
Length at age 0 years fixed (L_0, cm)	Fixed	3.0	
Asymptotic length (L_∞, cm)	Normal	70 .0 (L) 40.0 (S)	10
Growth coefficient (K) determined from $1.5^{-1}M$ with 10% variation	Variable	$M1.5^{-1}$	16
C.V. (Length at age)	Normal	0.1	40

Movement			
Minimum age (years) move (A_{min})	Uniform	3.000 (L) 1.500 (S)	19.0
Rate of movement at A_{min}	Uniform	0.225	45.0
Maximum age (years) move (A_{max})	Uniform	10.000 (L) 4.500 (S)	11.5 (L) 19.0 (S)
Rate of movement at A_{max}	Uniform	0.745	19.0
Fishery			
Annual fishing mortality	log-normal	M	6 (L) 16 (S)
Beginning length at 100% selected in juvenile area ($L_{100\%\mathrm{S,area1}}$)	Normal	$3^{-1}L_\infty$	10
Ascending width in log space in juvenile area	Variable	$\ln[-(L_{100\%\mathrm{S,area1}}{}^{2})(\ln 0.01)^{-1}]$	10
Descending width in log space in juvenile area	Fixed	8	
Beginning length at 100% selected in adult area ($L_{100\%\mathrm{S,area2}}$)	Normal	$2(3)^{-1}L_\infty$	5
Ascending width in log space in adult area	Variable	$\ln[-(L_{100\%\mathrm{S,area2}}{}^{2})(\ln 0.01)^{-1}]$	5
Descending width in log space in adult area	Fixed	8	