Fisheries Research 180 (2016) 113–118

Contents lists available at ScienceDirect

Fisheries Research

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

Estimating fish growth for stock assessments using both age–length and tagging-increment data

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ARTICLE INFO

Article history:
Received 27 February 2015
Received in revised form 3 June 2015
Accepted 16 June 2015
Available online 2 July 2015

Keywords:
Growth
Age–length data
Tagging-increment data
Stock assessment

ABSTRACT

In age-structured stock assessments it would be useful to be able to include all available information on growth, including age–length observations and length increments from tagging experiments. However, it was suggested in 1988 that combing the growth information from these two sources was problematic because the age- and length-based growth information they contain are not directly comparable. We evaluate two approaches that have since been made to this problem and conclude that though both approaches achieve comparability the simpler method was better suited for use in stock assessments, in part because of lesser computational demands. We show how the simpler approach is improved by allowing for correlation between length deviates at tagging and recapture, which increases biological plausibility and corrects a negative bias in estimates of variability in length at age.

1. Introduction

In recent years much of the research into fish biology has been driven by the requirements of the stock assessment models that inform the management of fisheries. One component of these models is fish growth – a mathematical description of how body length increases with time. Three main types of data can be used to construct this mathematical description: age–length (observations of the age and length of each fish in a sample); tagging-increment (observations of length and date at tagging and recapture from a mark-recapture experiment); and length composition (observations of fish length in annual catch samples from a fishery or survey). In this study our focus is on the problem of combining growth information from the first two of these. The problem is particularly relevant for tropical tunas, where age–length data, which use counts of otolith daily rings, are available only for young fish, and so need to be combined with tagging-increment data (Aires-da-Silva et al., 2015) to extend the range of ages covered.

Francis (1988) identified a *comparability problem* associated with growth estimates from these two types of data: those from age–length data are age-based, and thus not directly comparable with the length-based estimates from tagging-increment data. It was shown that the then current way of combing these two information types (using the equation of Fabens, 1965) implicitly assumed that the expected growth rate of fish of age A is the same as that of fish of length $\bar{L}_A$, the mean length at age A. It might be thought that, although this assumption may not be exactly true, perhaps it would be sufficiently close to the truth to be a useful approximation. That seems plausible for younger fish (as in Fig. 1a), but as A increases, the range of ages for fish of length $\bar{L}_A$ widens dramatically (Fig. 1b), and the assumption seems less and less tenable. Moreover, although it is possible to estimate, from tagging-increment data, a growth rate for fish whose length L exceeds the (age-based) asymptotic mean length, L_∞, there is no way to convert this estimate to an age-based growth rate because there is no age A for which $\bar{L}_A = L$ in this case (Fig. 1c). As a consequence, an estimate of L_∞ from tagging-increment data tends to be closer to the maximum length, rather than the asymptotic mean length defined in age-based growth.

Another important stock assessment desideratum is that the estimation of growth should, where possible, be done within the stock assessment model. In earlier times, growth parameters were estimated outside the model, and then held fixed in the stock assessment model while other population parameters were estimated. This was found to be unsatisfactory, and the philosophy of integrated analysis was developed (Fournier and Archibald, 1982; Maunder and Punt, 2013), which required, as much as possible, the inclusion of raw data into the stock assessment model, rather than fixed parameters estimated from these data. In the present context

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http://dx.doi.org/10.1016/j.fishres.2015.06.011
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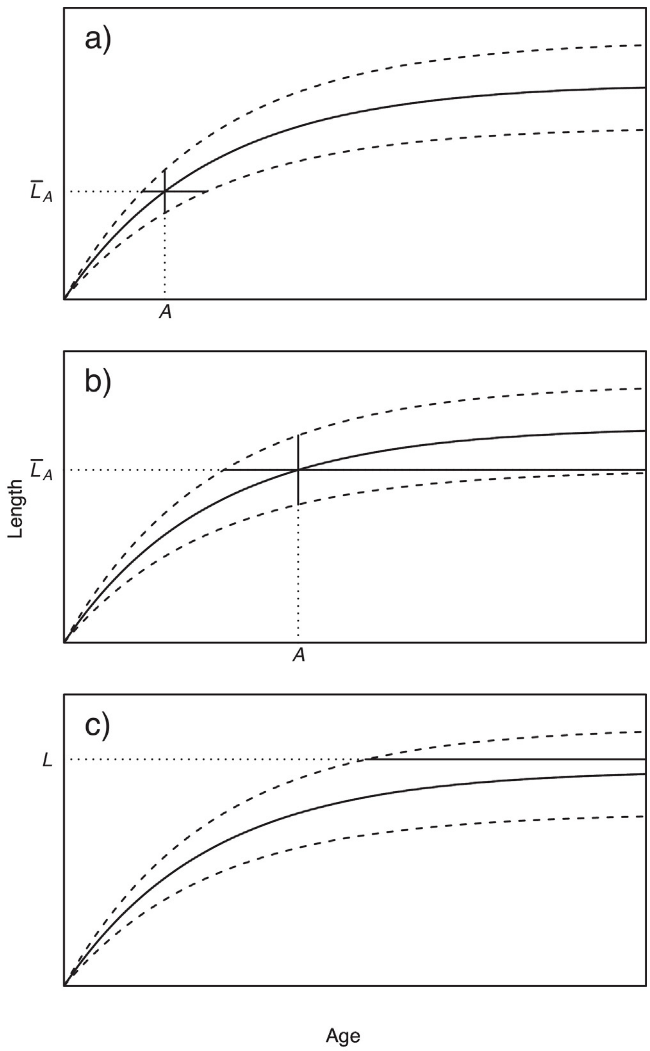

Fig. 1. Illustration of the implicit assumption involved in a conventional method of combining age-based growth estimates (from age–length data) with length-based estimates (from tagging-increment data). In each panel, the solid curved line describes the mean length at age and the dashed curved lines are 95% confidence bounds for length at age; the vertical line segment covers most fish of age A, and the horizontal segment covers most fish of length L, where $L = \bar{L}_A$, the mean length at age A: (a) for younger fish; (b) for older fish and (c) when $L > L_\infty$ (in which case there is no age A such that $L = \bar{L}_A$).

this requirement means that the methods of estimating growth parameters should not be too computer intensive.

In this study we evaluate two recent approaches to the problem of combining age–length and tagging-increment data, considering them both in relation to the two above-mentioned problems (that identified by Francis (1988), and the needs of integrated analysis), and also with respect to other criteria elaborated below. We label these two approaches by the initials of their authors. The first, LEP (after authors Laslett, Eveson, and Polacheck), is described in Eveson et al. (2004), which is one of a remarkable series of papers considering several related problems associated with growth (see also Laslett et al., 2002, 2004a,b and Eveson et al., 2007). The second approach, AMSF (after Aires-da-Silva, Maunder, Schaefer and Fuller), suggested by Aires-da-Silva et al. (2015), modified and simplified the LEP approach. We make no attempt to describe these approaches in detail, but instead restrict attention to the aspects that are most relevant to our enquiry. Thus we ignore matters that are important in estimating growth from a single data type (e.g., ageing error and the effect of tagging on growth) but not relevant to the problem of combining growth information from different data types.

2. The LEP approach

There are two features of this approach that are important to us. First, a *random-coefficients model* is assumed for growth. In its most general form this means that all individual fish growth is assumed to follow the same parametric form, with each fish having its own parameter values (so the parameter values are considered to be randomly distributed within the population). In the LEP approach a slightly simpler form is used in which one parameter, the asymptotic length, L_∞, is treated as random, while each of the other parameters (in a vector $\boldsymbol{\theta}$) is assumed to have a common value for all fish. (As a specific example they suppose that the parametric form used is the von Bertalanffy equation, $L = L_\infty[1 - \exp(-k(A - t_0))]$, so $\boldsymbol{\theta}$ is the pair of parameters k and t_0). The second important feature concerns how tagging-increment data are fitted within this model (the fitting of the age–length data is straightforward and uncontroversial in the present context). This is done using *random effects*. Specifically, in the von Bertalanffy example, for each tagged fish, L_∞ and A_{rel} (the relative age at tagging, defined by $A_{rel} = A_{tag} - t_0$) are treated as random effects. That is to say, rather than estimating individual values of L_∞ and A_{rel}, we integrate over all possible values of these and just estimate the parameters of their distributions (e.g., $\mu_{L\infty}$ and $\sigma_{L\infty}$, the mean and standard deviation of the distribution of L_∞, which is assumed to be normal).

From a mathematical and statistical point of view the LEP approach is elegant and impressive. In particular, it cleverly avoids the comparability problem of Francis (1988) by treating the pair of observed lengths (L_{tag} and L_{rec}) as a function of age, A_{rel}, so their growth estimate is age-based (in contrast, the conventional [length-based] approach treats the observed growth increment, $L_{rec} - L_{tag}$, as a function of L_{tag}).

However, the LEP approach has, from the present perspective, some significant weaknesses. As Aires-da-Silva et al. (2015) noted, it is too computation-intensive to include in stock assessment models and the random coefficients assumption is inconsistent with the usual growth assumptions in these models (which are described in the next section). Assuming random L_∞, and fixed k and t_0, implies that variation in length at age has a constant coefficient of variation, which is a less flexible assumption than used in many stock assessments (Francis, 2016), Finally, the LEP approach also falls on the wrong side of Occam's razor, in that it makes more detailed assumptions than can be supported by the data to which it is fitted [each fish is observed on just one (for age–length data) or two (for tagging-increment data) occasions, so we have no way of using these data to test the very strong assumption that the growth curves of all individuals in a population share a common smooth parametric form].

3. The AMSF approach

Aires-da-Silva et al. (2015) modified the LEP approach by dropping the random coefficients growth model. Their growth model has exactly the same components as are routinely included in age-structured stock assessment models, viz, (i) an equation describing mean length as a function of age, (ii) an equation describing variability in length at age as a function of age, and (iii) and an assumed statistical distribution for variability in length at age (Francis, 2016). These components are illustrated by the curved lines (solid and dashed) in Fig. 1. As with the LEP approach, the fitting of age–length data to this model is straightforward, but the fitting of tagging-increment data needs to be discussed. The latter involves, for each tagged fish, estimating the age at tagging, A_{tag}, as a