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A new proportionality-based back-calculation approach, which employs traditional forms of growth equations, improves estimates of length at age

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Abstract

The performance of a new proportionality-based back calculation approach, describing the relationship between length, otolith size and age using traditional growth curves and assuming a bivariate distribution of deviations from those curves, was evaluated. Cross-validation was used for six teleost species to compare predictions of expected lengths or otolith sizes at age, given otolith size or length, respectively, with those of other proportionality-based approaches that incorporate age. For four species, and particularly *Acanthopagrus butcheri* when using a biological intercept, better estimates were produced using the new model than were produced using the regression equations in the other back-calculation approaches. Back-calculated lengths for *A. butcheri* estimated using this model were more consistent with observed lengths, particularly when employing a biological intercept, than those obtained using other proportionality-based approaches and also a constraint-based approach known to produce reliable estimates. By selecting somatic and otolith growth curves from a suite of alternatives to better describe the relationships between length, otolith size, and age, the new approach is likely to produce more reliable estimates of back-calculated length for other species.

Résumé

La performance d’une nouvelle approche de rétro-calcul à base proportionnelle, décrivant la relation entre la longueur des poissons, la taille des otolithes et l’âge à l’aide de courbes de croissance traditionnelles et en supposant une distribution bivariée des déviations de ces courbes, a été évaluée. La validation croisée a été utilisée, pour six espèces de téléostéens, afin de comparer les prédictions de longueurs de poissons ou tailles des otolithes attendues à l’âge, compte tenu de la taille des otolithes ou de la longueur des poissons, respectivement, avec celles d’autres approches à base proportionnelle qui incorporent l'âge. Pour quatre espèces, et en particulier pour *Acanthopagrus butcheri* lors de l'utilisation d'un intercept biologique, les estimations produites à l'aide du nouveau modèle étaient meilleures que celles produites par les régressions des autres approches de rétro-calcul. Les longueurs obtenues par rétro-calcul pour *A. butcheri* à l'aide du nouveau modèle étaient plus compatibles avec les longueurs observées, particulièrement lorsqu'un intercept biologique était employé, que celles obtenues en utilisant d'autres approches à base proportionnelle ou qu'une approche à base de contraintes connue pour ses estimations fiables. En sélectionnant des courbes de croissance somatiques et des otolithes à partir d'une suite de courbes alternatives pour mieux décrire les relations entre la longueur des poissons, la taille des otolithes et l'âge, la nouvelle approche est susceptible de produire des estimations de rétro-calcul de longueur plus fiables pour d'autres espèces de poissons.

Keywords

Cross-validation; biological intercept; fish length-otolith radius relationship; bivariate growth model

Introduction

Back-calculation is an invaluable tool used by fisheries scientists around the world for reconstructing individual growth histories of fish from the microstructures present within their hard body parts, such as otoliths (e.g., Campana 1990, 2005; Vigliola and Meekan 2009). The development of a back-calculation model is a two-step process, which involves 1) fitting an appropriate regression equation to describe the relationship between fish length, otolith size and, in some recent approaches, age (Morita and Matsuishi 2001; Finstad 2003), and 2) developing a back-calculation formula which, using the results of the regression analysis, may be used to estimate the lengths of individual fish at a given age (Francis 1990; Vigliola and Meekan 2009). If a proportionality-based back-calculation approach is to produce reliable back-calculated estimates of length, the regression equations, fitted in the first of these two steps, must produce accurate estimates of the expected length or otolith radius for a fish, given observed values for its independent variables. Although several studies have attempted to validate the final lengths estimated using various back-calculation formulae (e.g., see Table 2 in Vigliola and Meekan 2009), apparently none has used cross-validation to directly explore the accuracy and precision of estimates of fish length and otolith radius at capture predicted by the regression equations fitted to those variables and age, prior to employing those equations in the back-calculation formulae.

Two main back-calculation methods, which have led to the development of different back-calculation formulae, emerge from the literature. The first approach assumes that, throughout the life of a fish, particular measurements of somatic and otolith size retain constant proportionality with respect to the values expected for fish within the population (e.g., Whitney and Carlander 1956; Francis 1990). The second approach constrains the equation relating length and otolith size for individual fish to pass through one or more points, e.g., a common intercept (e.g., Campana 1990; Vigliola and Meekan 2009). More recently-developed proportionality-based back-calculation approaches, such as those of Morita and Matsuishi (2001) and Finstad (2003), also recognise the influence of age in the relationship between fish length and otolith size. Constraint-based back-calculation approaches, such as the 'biological intercept' method proposed by Campana (1990), were developed to improve the accuracy of predicted lengths for younger fish and to reduce the influence on the reliability of lengths estimates of variation in somatic growth rate, where slow-growing fish have larger otoliths than faster growing fish of the same size, i.e., the growth effect. The biological intercept method assumes a common fish length and otolith size for fish at "the initiation of proportionality between fish and otolith growth" and, when employed in back-calculation, is typically taken to be the length and otolith size of newly-hatched fish.

In their recent review, based on theoretical considerations and on the results of a comparative study by Wilson et al. (2009), Vigliola and Meekan (2009) recommended use of the constraint-based approach of Fry (1943), as modified by Vigliola et al. (2000) and which uses the Biological Intercept, as this better accommodated possible allometry of fish length and otolith size than the Biological Intercept model of Campana (1990). Theoretically, Vigliola and Meekan (2009) based their decision on a requirement that the back-calculation formula must (1) assume proportionality of otolith-fish growth, and (2) generate realistic estimates of sizes at age (through use of a biological intercept). The former requirement, which was expressed mathematically as

$$\frac{d(L-a)}{(L-a)dt} = c\frac{dR}{Rdt},$$

where L and R represent the length and otolith radius of a fish, a is the body length when $R = 0$, and c is the constant of proportionality, is more restrictive than either of the assumptions of the Scale and Body Proportional Hypotheses (SPH or BPH). These last hypotheses describe the relationships between the particular measurements of length or otolith size for individual fish and the average values of expected length or otolith size for fish within the population given the observed values of the other variables, i.e., otolith size and fish length, respectively. They impose no specific constraint on the mathematical form of the equation(s) relating fish length and otolith size throughout the lives of the fish in the population, leaving this to be determined by the mathematical forms of the regression equations used to represent the relationships between those variables. In contrast, the criterion of Vigliola and Meekan (2009), as expressed in the above equation, specifies not only the proportionality between measures for each fish and those expected for the population but also the form of the relationship between the expected values of variables over the lives of the fish in the population. As the processes of fish and otolith growth differ, with the latter also involving the physico-chemical process of accretion of material on the surfaces of the otoliths, the relationship between the relative growth rates of the fish and their otoliths is likely to vary throughout life. It is thus suggested that it is the extent to which the regression equations accurately describe the relationships between fish and otolith size that should be the criterion for acceptance rather than the strict requirement that those regression equations are consistent with above differential equation of Vigliola and Meekan (2009).

Although models based on the SPH or BPH do not constrain the trajectories of length and otolith radius for individual fish such that these pass through a specific, pre-determined biological intercept, the functions describing the relationships between expected length and otolith radius and covariates can be constrained to pass through such an intercept. This would reduce the influence of the growth effect on estimates of back-calculated length, thereby addressing the second requirement of Vigliola and Meekan (2009), i.e., that realistic estimates of sizes at age are produced by the approach. The introduction of such constraints into the regression equations of the proportionality-based back-calculation approaches requires further exploration, however, as it will affect the estimates of the expected values of fish length and otolith size produced by those equations.

All back-calculation formulae assume a relationship between fish and otolith growth (Vigliola and Meekan 2009), typically describing that relationship by a function that directly relates those variables. None of the regression equations employed in existing back-calculation approaches appears to recognise explicitly, however, that the allometric relationship between fish lengths and otolith sizes for individual fish is the result of the somatic and otolith growth that those fish have experienced. Note also that, although otolith growth is essentially a physico-chemical process, it is partially governed by fish metabolism and thus the two growth curves are not independent. Through explicit incorporation of these growth equations in the descriptions of fish length-otolith size allometry, it will be possible to draw on the very considerable body of knowledge of somatic growth, and factors that affect this, to improve back-calculation approaches and better inform growth studies. A bivariate growth model developed by Ashworth et al. (in press) , which links the predictions of somatic and otolith growth curves for fish of the same age, offers an opportunity to explore how such a model might be extended for use in a proportionality-based back-calculation approach and to examine how its estimates compare with those of various existing approaches.

The overall objective of this study was to develop a proportionality-based back-calculation approach based on the bivariate growth model (Ashworth et al., in press), and to assess whether, for one selected species, the back-calculated estimates of length produced by this model are equally reliable, or more reliable, than those produced by other contemporary back-calculation approaches. Firstly, the bivariate growth model and the regression models described by Morita and Matsuishi (2001) and Finstad (2003), which also included age when predicting expected otolith size, were fitted to fish lengths and otolith sizes at capture for individuals from each of six fish species with differing biological characteristics. Cross-validation was then employed to compare the accuracy and precision of estimates of expected length and otolith radius at capture calculated using the different fitted models when applied to data for fish that had been excluded when fitting those models. Secondly, data for one species (*Acanthopagrus butcheri*) were used to test, using cross-validation, whether constraining the various models to pass through a biological intercept improved their predictive performance in estimating lengths and otolith radii at capture, and ascertained whether the bivariate growth model performed better than other approaches. Finally, the three proportionality-based back-calculation approaches, i.e., the fitted bivariate growth model and the approaches of Morita and Matsuishi (2001) and Finstad (2003), both with and without constraining the curves to a biological intercept, and the constraint-based approach of Vigliola et al. (2000), were used to estimate lengths at ages associated with opaque zones delineated prior to the age at capture (subsequently termed 'age at zone') for *A. butcheri*, which were then compared.

Material and Methods

1.1 The six study species

Data for six fish species from different families and environments, and with varying life cycle characteristics were used for this study. The species, which were studied, were the sparid Black Bream, *Acanthopagrus butcheri* (Munro 1949); the sciaenid Mulloway, *Argyrosomus japonicus* (Temminck and Schlegel 1843); the labrid Foxfish, *Bodianus frenchii* (Klunzinger 1880); the serranids Breaksea Cod, *Epinephelides armatus* (Castelnau 1875), and Goldspotted Rockcod, *Epinephelus coioides* (Hamilton-Buchanan 1822); and the glaucosomatid West Australian Dhufish, *Glaucosoma hebraicum* Richardson, 1845. Maximum ages and total lengths of these species ranged from ~ 19 to 78 years and from

~ 480 to 2 000 mm, respectively, with habitats extending from temperate estuaries to tropical marine waters[1].

During the present study, 128 *A. butcheri* were collected in May 2013 from the Wellstead Estuary at 34°50’S latitude and 118°60’E longitude on the south coast of Western Australia. This study was conducted in accordance with conditions in permit R2561/13 issued by the Murdoch University Animal Ethics Committee. For the five other species, permits were issued during earlier studies by the Murdoch University Animal Ethics Committee. Details of date and location of capture for each of these five species can be found in Table S2.

1.2 Fish processing and otolith measurements for six species, and biological intercept for **Acanthopagrus butcheri**

The total length (TL) of each *A. butcheri* was measured to the nearest 1 mm and its two sagittal otoliths removed and stored. High-contrast digital images of the sectioned otoliths (i.e., the left sagittal otolith) of each individual were taken under reflected light and analysed using the computer imaging package Leica Application Suite version 3.6.0 (Leica Microsystems Ltd. 2001) (for details regarding the sectioning of otoliths refer to Ashworth et al. (in press)). The ages for *A. butcheri* were determined for each fish from the number of opaque zones in a section from its otolith, its date of capture, and the birth date assigned to *A. butcheri* in the Wellstead Estuary (corresponding to the approximate mid-point of the spawning season) (Sarre and Potter 2000). Opaque zones in otoliths of *A. butcheri* were counted independently and on different occasions by E. Ashworth and P. Coulson. On the few occasions when the counts of these two readers differed (< 4%), the two readers discussed the basis for the discrepancy and determined a mutually agreed value which was used in following analyses.

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[1] Tables S1 and S2

Sectioned otoliths from 50 individuals of each of the other five species were randomly selected from the otoliths collected in previous studies in Western Australia by staff and research students at Murdoch University[2]. Preparation of these sections had followed the same procedure as that used for *A. butcheri*. The lengths recorded for, and ages assigned to, the individuals of each species in those earlier studies were accepted for use in the current study. Note that a common sample size of 50 randomly-selected fish of each species, other than *A. butcheri*, was used to facilitate comparability among results.

For all species, the 'radius' of each otolith, i.e., the distance between the primordium and the outer edge of the sectioned otolith, was measured under reflected light on three occasions to the nearest 0.1 µm along a line perpendicular to the opaque zones near the posterior edge of the sulcus acusticus of the otolith. The mean of these three measurements for each otolith was used as the radius of that otolith in subsequent analyses. In the case of *A. butcheri,* the distance along the same axis from the primordium of each otolith to the outside edge of the first opaque zone and the increments between the outside edges of successive opaque zones were also measured. For this species, the relative distinctness of the opaque zones in its otoliths made it possible to accurately measure the widths of increments between the outer margins of successive opaque zones.

For *A. butcheri*, eggs from the Australian Centre for Applied Aquaculture Research (ACAAR, Challenger Institute of Technology, Western Australia) were hatched overnight in the laboratory at Murdoch University to provide data to be used when employing a biological intercept (BI) in back-calculation models. Two days after hatching, the TLs of thirty randomly-selected larvae were measured to the nearest 0.01 mm under transmitted light. The left sagittal otolith of each larvae was collected and measured under a high-resolution digital microscope camera Leica DFC 425 (Leica Microsystems Ltd. 2001) mounted on a high-

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[2] Table S2

performance dissecting microscope Leica MZ7.5 (7.9:1 zoom). The radii of these whole otoliths were measured to the nearest 0.1 µm under transmitted light using the computer imaging package Leica Application Suite version 3.6.0.

1.3 Bivariate growth model and associated back-calculation approach

The bivariate growth model (Ashworth et al. (in press)) employed in this study, comprising both somatic and otolith growth curves and a bivariate statistical distribution of deviations, was fitted using an objective function written for Template Model Builder (package ‘TMB’, Kristensen 2015), in combination with the function ‘nlminb’, within R (R Development Core Team 2011) as described in Ashworth et al. (in press). For both fish lengths and otolith radii, the expected size at age *t*, i.e., $S(t)$, is represented in this model by either a modified version of the von Bertalanffy equation with an oblique linear asymptote or a form of the versatile growth curve described by Schnute (1981).

The modified von Bertalanffy equation is:

$$S(t) = g_S\left(t \middle| S_{\tau_1}, S_{\tau_2}, a_S, b_S\right) = c\{1 - \exp[-a_s(t - b_s)]\} + d(t - b_s),$$

where

$$c = \frac{y_2/(\tau_2 - b_s) - y_1/(\tau_1 - b_s)}{\{1 - \exp[-a_s(\tau_2 - b_s)]\}/(\tau_2 - b_s) - \{1 - \exp[-a_s(\tau_1 - b_s)]\}/(\tau_1 - b_s)},$$

and

$$d = \frac{y_1 - c\{1 - \exp[-a_s(\tau_1 - b_s)]\}}{\tau_1 - b_s}.$$

The Schnute (1981) model, which comprises the following four equations, is:

$$S(t) = g_S\left(t \mid S_{\tau_1}, S_{\tau_2}, a_S, b_S\right) = \begin{cases} \left[S_{\tau_1}^b + (S_{\tau_2}^b - S_{\tau_1}^b)\dfrac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}}\right]^{b^{-1}} & \text{if } a_S \neq 0, b_S \neq 0 \\ S_{\tau_1} \exp\left[\ln\left(\dfrac{S_{\tau_2}}{S_{\tau_1}}\right)\left(\dfrac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}}\right)\right] & \text{if } a_S \neq 0, b_S = 0 \\ \left[S_{\tau_1}^b + (S_{\tau_2}^b - S_{\tau_1}^b)\left(\dfrac{t - \tau_1}{\tau_2 - \tau_1}\right)\right]^{b^{-1}} & \text{if } a_S = 0, b_S \neq 0 \\ S_{\tau_1} \exp\left[\ln\left(\dfrac{S_{\tau_2}}{S_{\tau_1}}\right)\left(\dfrac{t - \tau_1}{\tau_2 - \tau_1}\right)\right] & \text{if } a_S = 0, b_S = 0 \end{cases}$$

where S_{τ_1} and S_{τ_2} are the expected sizes at two specified reference ages τ_1 and τ_2, and a_S and b_S are parameters that determine the shape of the curve. The minimum and maximum ages at capture of each species were used as the reference ages τ_1 and τ_2 in this study.

For each of the analyses undertaken in this study, the data were separated into two subsets, the first of which was used when fitting the bivariate growth or regression models, and the second for which expected lengths of the fish, given their observed values of otolith radii at given ages, were predicted using the fitted models. The bivariate growth model was fitted simultaneously to length and otolith size at capture, using age as an explanatory variable, to obtain estimates of the parameters of the somatic and otolith growth curves (Ashworth et al. (in press)). Deviations of observed fish lengths and associated otolith radii at capture from those respective growth curves were assumed to possess a bivariate normal, normal-lognormal, lognormal-normal, or bivariate lognormal distribution (Appendix S3 in Ashworth et al. (in press)).

When predicting the expected length of each fish at age using the bivariate growth model, the estimate calculated using the somatic growth curve was adjusted using information from the deviation of the observed from the predicted radius of the otolith. For this, the length at age predicted using the somatic growth curve was adjusted to the mean of the conditional distribution of the lengths at that age given the deviation between the observed and predicted otolith radii and the bivariate distribution of the deviations of lengths and otolith radii (equations for calculating the conditional distribution of each of the two variables of the various bivariate statistical distributions are presented in Ashworth et al. (in press)). Likewise, the estimates of expected otolith radii at age were obtained by adjusting the values predicted using the otolith growth curve to the values of the conditional means of the radii at age given the deviations between the observed lengths at age and the expected lengths at age predicted using the somatic growth curve. The resulting estimates of the lengths at age *t* given the observed otolith radii at those ages, i.e., $\hat{L}_{t|R_t=R^*}$, and otolith radii at age given the observed fish lengths at those ages, i.e., $\hat{R}_{t|L_t=L^*}$, were then used in the subsequent cross-validation and back-calculation sections of this study. Observed and expected lengths and otolith radii at age *t* are denoted by L_t, $\hat{L}_t$, R_t, and $\hat{R}_t$, respectively, and particular observed values of length and radius by L^* and R^*, respectively.

A modified form of the bivariate growth model, in which somatic and otolith growth curves were constrained to pass through the biological intercept, was also fitted to the lengths and otolith radii at capture for *A. butcheri*. For this, τ_1 was set to the age of the fish used when calculating the biological intercept, and L_{τ_1} and R_{τ_1} were set to the total fish length and otolith radius at the biological intercept, thereby reducing the number of parameters to be estimated when fitting the bivariate model.

For back-calculation of lengths of *A. butcheri* using the bivariate growth model, it was assumed that the proportional deviation of fish length at capture from the expected length given the observed otolith radius at that age remained constant throughout life. Accordingly, an estimate of the length of fish *j* with age at zone t_k, i.e., L_{j,t_k}, was calculated as

$$L_{j,t_k} = \frac{\hat{L}_{t_k|R_{t_k}=R_{j,t_k}}}{\hat{L}_{t_c|R_{t_c}=R_{j,t_c}}} L_{j,t_c},$$

where L_{j,t_c} and R_{j,t_c} are the length and otolith radius at age t_c when the fish was caught, and R_{j,t_k} is the otolith radius at the edge of opaque zone *k*.

1.4 Proportionality-based and constraint-based back-calculation approaches

The accuracy and precision of lengths and otolith radii predicted using the above bivariate growth model were compared with those predicted using the regression models (or derived from or based on those models) of the proportionality-based back-calculation approaches described by Morita and Matsuishi (2001) and Finstad (2003) (Table 1). The Morita and Matsuishi (2001) 'age effect' (AE) model employs age at capture in the relationship between otolith size and fish length, while the 'interaction term' (IT) model of Finstad (2003) extends the Morita and Matsuishi (2001) model by incorporating an interaction between fish length and age at capture. Vigliola and Meekan (2009) reported a modified form of the 'age effect' model that employs fish length and otolith size as the dependent and independent variable, respectively, terming this the 'age effect Body Proportional Hypothesis' or AEBPH model. For this study, the 'interaction term' model was re-arranged and an analogous form of model developed to express fish length in terms of otolith size (Table 1). These have been termed a 're-arranged interaction term' (RIT) model, and an 'analogous interaction term' (AIT) model, respectively. The regression equations of the proportionality-based back-calculation approaches of Morita and Matsuishi (2001) and Finstad (2003), and those derived from or based on those regression equations, were also re-written as equations constrained to pass through the biological intercept (Tables 1 and 2).

A further analysis compared back-calculated estimates of lengths produced for *A. butcheri* using the proportionality-based back-calculation approach developed using the bivariate growth model with those calculated using the approaches described by Morita and Matsuishi (2001) and Finstad (2003), and the constraint-based back-calculation model described by Vigliola et al. (2000). Only published versions of these traditional back-calculation formulae, and versions of these constrained to pass through the biological intercept, were used. Details of the various back-calculation approaches are presented below.

The back-calculation formula (with modified notation) of the ‘age effect’ model of Morita and Matsuishi (2001), which employs the parameters (i.e., α, β and γ) estimated using the regression equation Eq. 1 (Table 1), is

$$(11)\qquad L^*_{j,k} = -\frac{\alpha}{\beta} + \left(L_{c,k} + \frac{\alpha}{\beta} + \frac{\gamma}{\beta} t_{c,k}\right)\frac{R_{j,k}}{R_{c,k}} - \frac{\gamma}{\beta}\, t_j,$$

while that of Finstad (2003), i.e., the ‘interaction term’ model, which uses the parameters (i.e., α, β, γ, and δ) as estimated by fitting Eq. 2 (Table 1), is

$$(12)\qquad L^*_{j,k} = \frac{\left[\left(\alpha + \beta L_{c,k} + \gamma t_{c,k} + \delta L_{c,k} t_{c,k}\right)\frac{R_{j,k}}{R_{c,k}} - \alpha - \gamma t_j\right]}{\beta + \delta t_j}.$$

$L^*_{j,k}$ is the back-calculated length of fish k with age at zone t_j, $L_{c,k}$ is the observed length of fish k at capture, i.e., at age $t_{c,k}$, $R_{j,k}$ is the observed radius of the otolith of fish k at age t_j, and $R_{c,k}$ is the observed radius of the otolith of fish k at capture.

The regression models employed by Morita and Matsuishi (2001) and Finstad (2003) were constrained to pass through the biological intercept by rewriting α as a function of the length, radius and age at that intercept using equations 1 and 2 (Table 1). The re-parameterised back-calculation formulae become

$$(13)\qquad L^*_{j,k} = -\frac{R_{BI} - \beta L_{BI} - \gamma t_{BI}}{\beta} + \left(L_{c,k} + \frac{R_{BI} - \beta L_{BI} - \gamma t_{BI}}{\beta} + \frac{\gamma}{\beta} t_{c,k}\right)\frac{R_{j,k}}{R_{c,k}} - \frac{\gamma}{\beta} t_j$$

and

(14)
$$L_{j,k}^{*} = \frac{\left\{ \left[R_{BI}+\beta\left(L_{c,k}-L_{BI}\right)+\gamma\left(t_{c,k}-t_{BI}\right)+\delta\left(L_{c,k}t_{c,k}-L_{BI}t_{BI}\right)\right]\frac{R_{j,k}}{R_{c,k}} \atop -\left(R_{BI}-\beta L_{BI}-\gamma t_{BI}-\delta L_{BI}t_{BI}\right)-\gamma t_{j} \right\}}{\beta+\delta t_{j}},$$

where R_{BI} = otolith radius at biological intercept (µm), L_{BI} = total length (mm) at biological intercept, and t_{BI} = age (years) associated with the biological intercept, and where the values of the parameters in Eq. 13 are obtained by fitting the regression model described by Eq. 6 (Table 2), and those in Eq. 14 by fitting the regression model of Eq. 7 (Table 2).

The back-calculation formula, i.e., modified Fry model, of Vigliola et al. (2000) is

(15)
$$L_{j,k}^{*} = \varphi + \exp\left[ln\left(L_{BI}-\varphi\right) + \frac{\left[ln\left(L_{c,k}-\varphi\right)-ln\left(L_{BI}-\varphi\right)\right]\times\left[ln\left(R_{j,k}\right)-ln\left(R_{BI}\right)\right]}{\left[ln\left(R_{c,k}\right)-ln\left(R_{BI}\right)\right]}\right]$$

where φ is the fish body length at otolith formation, with $\varphi = \frac{\varphi_1+\varphi_2}{2}$, $\varphi_1 = L_{BI} - \beta_1 R_{BI}^{\gamma_1}$, and $\varphi_2 = L_{BI} - \beta_2 R_{BI}^{\gamma_2}$, and where γ_1, β_1, γ_2, and β_2 are parameters estimated by fitting the following regression equations (Vigliola and Meekan 2009) to observed fish lengths and otolith radii at capture.

(16)
$$L = L_{BI} - \beta_1 R_{BI}^{\gamma_1} + \beta_1 R^{\gamma_1}$$

(17)
$$R = \left(\frac{L - L_{BI} + \beta_2 R_{BI}^{\gamma_2}}{\beta_2}\right)^{\frac{1}{\gamma_2}}$$

1.5 Analyses

All analyses were undertaken using R (R Development Core Team 2011).

1.5.1 Ten-fold cross-validation and hold-out validation

Two cross-validation methods, i.e., a ten-fold cross-validation and a hold-out cross-validation (Kohavi 1995; Then et al. 2015), were employed in this study to assess the predictive performance of the regression equations of the different proportionality-based back-calculation approaches. That is, they were used to assess the ability of those equations to produce predictions of length and otolith radius at capture that matched the measured values for fish, data for which had been excluded when fitting the regression equations. Such comparison differs from comparisons that employ likelihood ratios or AICs, which assess the extent to which predicted values match observed values of a dependent variable for data included when fitting the model. Note that cross-validation was employed only to assess the ability of the regression equations of the back-calculation approaches to produce accurate predictions of expected lengths and otolith radii, given known values of the independent variables of the regression equation, but not to assess the validity of the back-calculation approach in predicting the lengths of individual fish at ages prior to their capture.

For the ten-fold cross-validation for each species, i.e., *A. butcheri*, *A. japonicus*, *B. frenchii*, *E. armatus*, *E. coioides* and *G. hebraicum,* the 50 fish in the sample used for the study described in Ashworth et al. (in press) were assigned randomly to ten groups. For each of the proportionality-based back-calculation approaches, the following analysis was undertaken using firstly the equation relating fish length to otolith radius and age at capture, and subsequently the equation for the relationship between otolith radius and fish length and age at capture. Excluding each of the ten groups in turn, the regression model was fitted to the data from the other nine groups and used to calculate the expected value of the dependent variable for each fish in the excluded group. Following Then et al. (2015), the Root Mean Square Error (RMSE) of the resulting predicted values of fish lengths and otolith radii from the corresponding observed values of those variables was employed as an overall measure of the predictive ability of the regression equation. This was calculated as $\mathrm{RMSE}=\sqrt{\frac{1}{n}\sum_{i=1}^{n} e_i^2}$, where e_i is the difference between the observed and predicted values of the dependent variable for observation i ($i = 1, 2, \ldots, n$) and n is the number of observations (Dunn et al. 2002; Chai and Daxler 2014). A measure of the bias of the predicted values from the corresponding observed values for the excluded fish was obtained by calculating the overall mean of the differences between the observed and expected values, i.e., the Mean Error $ME = \frac{1}{n}\sum_{i=1}^{n} e_i$ (Walther and Moore 2005).

The above cross-validation analysis was undertaken separately for the bivariate growth model and each of the alternative proportionality-based back-calculation approaches, i.e., the 'age effect', 'interaction term', AEBPH, 're-arranged interaction term', and 'analogous interaction term' models (Tables 1 and 2). The difference between the RMSE calculated for each alternative model and that for the bivariate growth model, expressed as a percentage of the latter, was calculated as

$$\%\Delta RMSE = 100\ (RMSE - RMSE_{bivariate\ model})/RMSE_{bivariate\ model}.$$

Ten-fold cross-validation was also undertaken, as described above for the samples of 50 fish from each species, using lengths and otolith radii for 120 individuals of *A. butcheri*, which had been randomly selected from the sample of 128 fish collected for this species. This procedure was repeated while constraining the length-otolith radius relationships to pass through the biological intercept, noting that *A. butcheri* was the only one of the six studied species for which such an intercept was available.

For *A. butcheri*, for which fish lengths and otolith radii and ages at capture had been recorded for 128 fish, the above ten-fold cross-validation was complemented with a hold-out validation (Kohavi 1995). This was undertaken by fitting each regression equation of the different back-calculation models to the data for the 50 *A. butcheri* used in the first of the ten-fold cross-validations, i.e., the 50 fish that had been used in the study reported in Ashworth et al. (in press), and using the resultant fitted equation to calculate the expected values of the dependent variables for the remaining 78 fish and, from these, the RMSE and ME of those deviations. As in the ten-fold cross-validation for the 120 fish, the holdout validation analyses were repeated for *A. butcheri* using the version of the bivariate growth model for which the somatic and otolith growth curves had been constrained to pass through the biological intercept, together with the regression equations of the other proportionality-based back-calculation approaches that had been similarly modified.

1.5.2 Back-calculation

Estimates of lengths at ages at zones were calculated for *A. butcheri* using the various proportionality-based and the constraint-based back-calculation formulae for both the case when the biological intercept was not included and the case when the model was constrained to pass through the biological intercept. For this, the bivariate growth model and various regression models of the different back-calculation approaches were fitted to the fish lengths, otolith radii and ages at capture for the 50 fish that had been used for the study reported in Ashworth et al. (in press). Using the resulting parameters, the back-calculation formulae of the different approaches were used to produce estimates of the length at each age at zone for each of the 78 *A. butcheri* that had been excluded in the preceding step when fitting the models, which were then compared. Mean lengths of *A. butcheri* within each age class of the sample were also calculated and compared with the means of the back-calculated lengths at the ages at zones bounding the otolith radii for those age classes.

Results

Accuracy and precision of length and otolith radius estimates for six species

Based on the results of the ten-fold cross-validation for 50 fish of each of the six species, the bivariate growth model produced lower estimates of RMSE for fish length than were obtained using the other models and thus improved prediction performance for all six species (Table 3*a*). In contrast, the re-arranged form of the interaction term model generally produced an estimate of RMSE (i.e., between 26 and 284) for fish length, which was greater (i.e., predictions with greater error) than was produced by either the bivariate growth model (RMSE = 17 to 87) or the Age Effect Body Proportional Hypothesis model (RMSE = 23 to 174) across all species. This was particularly the case for *E. coioides* and *G. hebraicum* for which the percentages by which the RMSEs of the re-arranged form of the interaction term model exceeded those of the bivariate growth model by as much as 241 and 353%, respectively. These large RMSEs appear to be due to occasional very small values of the denominator in Eq. 4 (Table 1), suggesting that this form of model may be sensitive to such values and, if employed in future studies, should be used with caution. Note that in the cases of *A. butcheri* and *G. hebraicum*, the analogous form of the interaction term model produced an estimate of RMSE for the length predictions similar (i.e., differing by only ~ 4%) to that obtained using the bivariate growth model (Table 3*a*). The bivariate growth model produced low values of positive and negative bias, and particularly in the cases of *A. butcheri* and *E. coioides* for which the model produced the lowest estimates of ME and observed lengths were either slightly overestimated or underestimated, respectively.

The bivariate growth model also produced better predictions of otolith radius for four of the six species, i.e., *A. butcheri*, *A. japonicus*, *E. armatus* and *G. hebraicum,* by providing values of RMSE lower than those calculated using the age effect and interaction term models (Table 3*b*). The predictions from the age effect model, in the case of *A. butcheri*, were nearly equal to those of the new model (differing by only ~ 1%) and provided as good a fit. The interaction term model, however, produced estimates of otolith radius for *B. frenchii* and *E. coioides* with lower (by ~ 5% and ~ 4%, respectively) RMSEs than those of the bivariate growth model. Although estimates of the ME were always very low and marginally different, the bivariate growth model did not produce the most accurate observed otolith radii compared with the age effect and interaction term models.

Accuracy and precision of length and otolith radius estimates for **Acanthopagrus butcheri***, with and without a biological intercept*

For the holdout validation for *A. butcheri*, the re-arranged form of the interaction term model produced length estimates with lower RMSEs (differing by ~ 2%) than were obtained using the bivariate growth model (Table 4*a*). In the case of the ten-fold cross-validation of 120 individuals of *A. butcheri*, however, the re-arranged form of the interaction term model was only marginally better (by < 1%) than the new bivariate growth model. When the models were constrained by the biological intercept, the bivariate growth model provided better predictions of lengths of *A. butcheri* for both the holdout (RMSE = 17) and the ten-fold cross-validation with 120 fish (RMSE = 17, Table 4*a*). Overall, when constraining the models to pass through the biological intercept, there was a slight decrease in the quality of the length predictions produced by the Age Effect Body Proportional Hypothesis, the re-arranged and the analogous forms of the interaction term models, i.e., for all cases other than that for the bivariate growth model with ten-fold cross-validation (Table 4*a*). The RMSE for predictions of length calculated using the bivariate growth model only improved slightly, i.e., by < 1%, when the biological intercept was imposed. In terms of accuracy, estimates of the ME matched those of the RMSE, such that the re-arranged form of the interaction term model and the bivariate growth model, which both produced lower RMSEs than the other models, also produced the most accurate observed lengths.

Low values of the RMSEs for the predictions of the otolith radii, with or without the biological intercept, indicated that the bivariate growth model was best for both the holdout and for the ten-fold cross-validation using 128 and 120 fish, respectively (Table 4*b*).

Although inclusion of the biological intercept slightly increased (by ~ 11%) the RMSEs of predicted otolith radii for the age effect model, a much greater (~ 8-fold) increase was produced in the RMSEs calculated using the interaction term model, suggesting that this latter model may occasionally be less robust depending on the data (or species). In the case of the holdout validation, the age effect model constrained to pass through the biological intercept produced estimates of predicted otolith radii that were least biased compared with predicted values produced by the other models, whereas, in the case of the ten-fold cross-validation with 120 fish, the interaction term model without the constraint of the biological intercept produced the most accurate estimates.

Comparison of length predictions for **Acanthopagrus butcheri** *from different back-calculation approaches*

Means of back-calculated lengths calculated using all of the proportionality-based approaches (without biological intercept) underestimated the mean observed lengths at age for the younger *A. butcheri* collected from the Wellstead Estuary (Table 5; Fig. 1). Thus, the means of the back-calculated total lengths of fish with age at zone = 3 years, which ranged from 161 (for the bivariate growth model) to 170 mm (for the interaction term model), were less than the mean observed length, i.e., 171 mm, for the fish with ages of 2.6 years at the date on which the sample was collected (May 2013). Although fish with ages between 3 and 6 years were not available in the sample, the bivariate growth model produced mean back-calculated estimates of length that were consistent with the means of the observed lengths for fish with ages > 6 years. The age effect model, however, only produced estimates of back-calculated length that were consistent with the observed lengths for fish with ages between 6 and 8 years, and > 10 years, the lengths for other ages were underestimated. The interaction term model only produced consistent estimates for fish aged from 6 to 8 years, underestimating the lengths of older fish. The modified Fry model produced estimates of back-calculated lengths that underestimated the means of the observed lengths for fish of all ages within the sample (Table 5).

The consistency of estimates of back-calculated lengths at the ages at each of the zones with means of observed lengths for fish with ages lying between the ages at those zones was improved by imposing the biological intercept as a constraint (Table 5; Fig. 1). In the case of the bivariate growth model, the means of the back-calculated estimates were consistent with the means of the observed lengths for *A. butcheri* of all observed ages. The estimates of the lengths calculated using the age effect back-calculation model were consistent with observed lengths for fish for all ages except 9 to 10 years, which were underestimated. Consistent length estimates were produced by the interaction term model only for fish with ages up to 7 years, but, for older fish, lengths were underestimated.

The age effect model produced estimates of lengths which were generally more similar to those calculated using the bivariate growth model than those obtained using the interaction term and modified Fry models, particularly at older ages (Fig. 1*a* and *b*). At young ages, however, back-calculated lengths estimated using the bivariate growth model (with biological intercept) were more comparable to those calculated using the modified Fry model (Table 5; Fig. 1*e*).

Discussion

Cross-validation of estimates derived from relationship between length, otolith radius and age

At the outset, note that it was not possible to apply the holdout or ten-fold cross-validation approaches to the modified Fry back-calculation formula of Vigliola et al. (2000).

This model assumes that, for an individual fish, the curve relating fish lengths and otolith radii passes through both the biological intercept and the length and otolith radius of the fish at capture.

Although the bivariate growth model is likely to produce more reliable predictions of length or otolith radius than the regression equations of the proportionality-based back-calculation approaches considered in this study, results are species-dependent. Evidence for this is provided by the finding that, although lengths at capture predicted by the bivariate growth model from otolith sizes and ages at capture for individuals of six fish species were more reliable than those produced using the regression equations of the back-calculation approaches, the model produced the most reliable predictions of otolith radii from fish lengths and ages at capture for only four of the six species. For the other two species, the regression equation of the interaction term back-calculation produced the lowest estimates of RMSE.

Cross-validation using 50 individuals, holdout validation using 128 individuals, and ten-fold cross-validation using 120 individuals of *A. butcheri* from the Wellstead Estuary demonstrated that, given fish lengths and ages, the most reliable estimates of otolith radii for this species were produced by the bivariate growth model, regardless of whether or not that model was constrained to pass through the biological intercept. Using the bivariate growth model with the biological intercept constraint, a similar result was obtained for estimates of fish length when ten-fold cross-validation was applied to the 50 randomly-selected individuals from the sample of 128 fish and when the larger datasets of 128 and 120 fish for were analysed using holdout and ten-fold cross-validation, respectively. When not constrained by the biological intercept, however, the regression equation of the re-arranged interaction term model produced the most reliable estimates of length for the holdout validation using 128 fish and the ten-fold cross-validation using 120 fish. Thus, without the constraint of the biological intercept, the results for the smaller sample were influenced by sample size. Given such inconsistency, it would therefore be appropriate to base predictions for *A. butcheri* on analyses employing models fitted to the larger of these datasets, i.e., the holdout cross-validation employing 128 fish or the ten-fold cross-validation using 120 individuals of this species. For this cross-validation, the most reliable estimates of fish lengths of *A. butcheri* given ages and otolith radii were obtained using the version of bivariate growth model that employed the biological intercept, while equally reliable estimates of otolith radii given ages and fish lengths were produced using the bivariate growth model with and without the biological intercept.

It was concluded above that, when constrained to pass through the biological intercept, the bivariate growth model is likely to provide the most reliable estimates of both fish lengths and otolith radii. This may be due to the considerable flexibility of the bivariate growth model, whereby the forms of the curves used to represent somatic and otolith growth are selected from the wide range of alternative forms described by the Schnute (1981) or modified von Bertalanffy growth models, and from alternative forms of bivariate statistical distributions for the distribution of deviations from those growth curves. This flexibility allows it to account for the particular characteristics of the relationships exhibited between observed fish lengths, otolith sizes and ages at capture of the individuals in the samples of the different species. In contrast, the linear regression equations, and the nonlinear regression equations produced by incorporating an interaction term or by re-arranging the linear equations are far more prescriptive. Although those latter models provide good descriptions of the allometric relationships between fish lengths, otolith sizes, and take into account the ages at capture for the sampled fish of the different species, their ability to adjust to the characteristics of the data are constrained by their fixed functional forms.

Prior to adopting a particular form of somatic growth curve, Katsanevakis and Maravelias (2008) recommended that a broad range of alternative growth curves should be explored when fitting to lengths at ages. The different approaches described in various back-calculation studies (e.g., Campana 1990; Francis 1990; Sirois et al. 1998; Vigliola et al. 2000; Morita and Matsuishi 2001), each employing slightly different equations to describe the relationships between length and otolith size (and, in some approaches, age at capture), reflect an awareness that the extent to which the different regression equations describe the data varies among samples from different species. The report by Vigliola and Meekan (2009) that as many as 22 different back-calculation approaches have been proposed suggests that a flexible approach, which identifies the most suitable form of regression equation, such as that used when fitting the bivariate growth model, is required to ensure that exploration of alternative model forms is undertaken using a systematic, well-defined procedure with explicit criteria for model selection.

The current study is apparently the first to employ cross-validation to explore the reliability of the values of fish length or otolith size predicted by the regression equations used in the different back-calculation approaches. Most earlier studies have only explored the extent to which predicted fish lengths associated with the various growth zones matched the means of the observed lengths of fish from the different age classes (e.g., Pierce et al. 1996; Sirois et al. 1998; Pajuelo and Lorenzo 2003; Zengin et al. 2006) or, in the few cases when recaptured tagged and otolith-marked individuals were available, the extent to which back-calculated estimates of length matched the lengths of the fish at release (e.g., Panfili and Tomás 2001; Roemer and Oliveira 2007; Li et al. 2008; Michaletz et al. 2009). These latter approaches are of considerable value, particularly those that validate back-calculated length estimates by comparison with lengths at tagging of recaptured, otolith-marked fish. Although cross-validation is unable to test the reliability of the final back-calculated estimates of lengths of individual fish, it offers the benefit to proportionality-based back-calculation approaches of elucidating the reliability of the expected lengths predicted for fish by the regression equations, on which the estimates of back-calculated lengths of individual fish rely.

Comparison of length predictions between back-calculation approaches

Back-calculated lengths at ages estimated for individuals of *A. butcheri* using the proportionality-based approach developed for the bivariate growth model were found to be very similar to those calculated using the three alternative traditional back-calculation formulae, i.e., the age effect, interaction term and modified Fry models. Overall, however, and particularly when using a biological intercept, length estimates produced using the bivariate growth model were more consistent with the observed mean lengths at age at capture than those based on the other approaches. These results suggest that, for some species other than *A. butcheri*, the proportionality-based bivariate growth approach developed in the current study will produce estimates of length at age that are more accurate than those produced by back-calculated traditional approaches.

To address potential bias resulting from continued increase in otolith size despite the reducing rate of somatic growth as fish age, the back-calculation approach developed by Morita and Matsuishi (2001) was the first to incorporate age as a predictor variable. Although this model produces less biased length estimates than earlier proportionality-based approaches for which growth rates of slow-growing fish were overestimated, it is also the least precise model (Morita and Matsuishi 2001). Indeed, large errors in predicted size produced by the age effect model were reported by Wilson et al. (2009), confirming the age effect model’s sensitivity to growth effects and to the accuracy and precision of the regression fitted to the relationship between fish length, otolith radius and age. Finstad (2003) found that incorporation of the interaction term into the age effect model contributed significantly to the quality of the fit of the length and otolith radius to age relationship, with difference between the two models being most pronounced in the youngest age classes. The results of the current study demonstrate that inclusion of the biological intercept improved the consistency of back-calculated length estimates with mean observed lengths for younger fish for both the age effect and interaction term models, thus overcoming to some extent the bias in predicted size introduced by these models (e.g., Vigliola and Meekan 2009; Wilson et al. 2009).

Wilson et al. (2009), who were the first to validate modern back-calculation models using longitudinal data collected and analysed at the individual level from multiple internal and external tagging trials, showed that, for two marine cleaning gobies *Elacatinus evelynae* and *Elacatinus prochilos*, the modified Fry model provided the most accurate (and least biased) size at age estimates despite the presence of age, growth and time-varying growth effects in the dataset. The better performance of the modified Fry model was explained by the allometric nature of the relationship between fish length and otolith size at the individual level, and that the model is constrained to biological intercepts (Vigliola et al. 2000; Wilson et al. 2009). Despite its complex form, the approach preferred by Vigliola and Meekan (2009) for use in routine back-calculation was the modified Fry model (Vigliola et al. 2000; Wilson et al. 2009). In the present study, however, back-calculated estimates of length at age from the bivariate growth model with the biological intercept constraint were closer to mean observed lengths at age than those produced by the modified Fry model, suggesting that, at least for *A. butcheri* from the Wellstead Estuary, the new approach may produce more accurate back-calculated estimates of fish length than the modified Fry approach.

The allometric relationship between fish length and otolith radius is formed by the changes in the sizes of these variables with age, throughout the life of the fish (Xiao 1996).

That is, the allometric relationship used in traditional back-calculation approaches integrates the effects of the growth of both variables. The bivariate growth model proposed in this study, on the other hand, explicitly describes the growth of each of these variables, offering greater opportunity to investigate the factors affecting that growth and thus, indirectly, the form of the relationship between length and otolith radius. The bivariate growth model may thus represent a valuable alternative to the modified Fry model as it provides a useful link between somatic and otolith growth models and back-calculation approaches, and a more realistic representation of the relationship between these variables, and age, through the life of fish.

For this study, as with the majority of other back-calculation studies, data for tagged and marked fish were not available. There would be value in comparing the performance of the proportionality-based bivariate growth approach against that of other back-calculation approaches using recaptures from an appropriate tagging study in which otoliths of individually-tagged fish have been chemically marked prior to their release, similar to the methods carried out by Panfili and Tomás (2001) and Li et al. (2008). It has been suggested that such tagging studies provide the most suitable data to validate the performance of a back-calculation formula (Casselman 1983; Vigliola and Meekan 2009).

To summarise and based on cross-validation results across a range of fish species, the RMSEs of predictions of expected fish length and otolith size produced by the new bivariate growth model were found typically to be equal to or better than those produced using the regression equations employed by the selected traditional back-calculation approaches considered in this study. The results of the analyses suggest that, for *A. butcheri* from the Wellstead Estuary, the expected length predicted for an individual fish based on its age and otolith size using the bivariate growth model is likely to be more reliable than those estimates produced using those other regression models, and thus likely to lead to more reliable estimates of back-calculated length. The proportionality-based back-calculation approach developed using the bivariate growth model, when constrained to pass through the biological intercept for this species, produced mean back-calculated length estimates that were more consistent with the mean observed lengths at age than those of other traditional back-calculation approaches. The results of this study strongly support the conclusion that back-calculated lengths calculated for *A. butcheri* in the Wellstead Estuary using the proportionality-based bivariate growth approach, and employing the biological intercept, are more reliable than those produced by the alterative back-calculation approaches that were considered. The approach is likely to be of value for other back-calculation studies, and may, as in the case of *A. butcheri*, provide estimates of back-calculated length that improve on those produced by traditional approaches.

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Table 1. Regression equations of the back-calculation approaches described by Morita and Matsuishi (2001), Finstad (2003) and Vigliola and Meekan (2009), or derived from those equations.

Eq.	Regression equation	Source
(1)	$R = \alpha + \beta L + \gamma t$	Morita and Matsuishi (2001)
(2)	$R = \alpha + \beta L + \gamma t + \delta L t$	Finstad (2003)
(3)	$L = \alpha + \beta R + \gamma t$	Re-arranged version of eq. 1 (AEBPH in Vigliola and Meekan 2009)
(4)	$L = (R + \alpha + \gamma t)/(\beta + \delta t)$	Re-arranged from eq. 2
(5)	$L = \alpha + \beta R + \gamma t + \delta R t$	Analogous linear form of eq. 2

Note. *R* = otolith radius (µm); *L* = total length (mm); *t* = age (years); α, β, γ, and δ = parameters of regression equation. AEBPH = Age Effect Body Proportional Hypothesis.

Table 2. Regression equations, which pass through the biological intercept, modified (or developed) from the equations of Morita and Matsuishi (2001), Finstad (2003) and Vigliola and Meekan (2009).

Eq.	Regression equation	Source
(6)	$R = R_{BI} + \beta(L - L_{BI}) + \gamma(t - t_{BI})$	Modified from eq. 1
(7)	$R = R_{BI} + \beta(L - L_{BI}) + \gamma(t - t_{BI}) + \delta\,(Lt - L_{BI}t_{BI})$	Modified from eq. 2
(8)	$L = L_{BI} + \beta(R - R_{BI}) + \gamma(t - t_{BI})$	Modified from eq. 3
(9)	$L = ([L_{BI}(\beta + \delta t_{BI}) - R_{BI} - \gamma t_{BI}] + R + \gamma t)/(b + \delta t)$	Modified from eq. 4
(10)	$L = L_{BI} + \beta(R - R_{BI}) + \gamma(t - t_{BI}) + \delta\,(Rt - R_{BI}t_{BI})$	Modified from eq. 5

Note. R_{BI} = otolith radius at biological intercept (µm); L_{BI} = total length (mm) at biological intercept; t_{BI} = age (years) associated with the biological intercept; R = otolith radius (µm); L = total length (mm); t = age (years); α, β, γ, and δ = parameters of regression equation.

Table 3*a*. Root Mean Square Error (RMSE) and mean error (ME) of total length estimates for the bivariate growth model and models derived from the Morita and Matshuishi (2001) and Finstad (2003) models calculated using ten-fold cross-validations for samples of 50 fish for each of *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides*, and *Glaucosoma hebraicum*. The percentages by which the RMSE of the alternative models differ from that of the bivariate growth model are presented in parentheses.

Species	Accuracy and precision measures	BG	AEBPH	RIT	AIT
Acanthopagrus butcheri	RMSE	**16.97**	22.90 (34.96)	29.53 (74.04)	17.69 (4.26)
	ME	0.08	-0.22	-2.98	0.25
Argyrosomus japonicus	RMSE	**87.36**	173.62 (98.74)	144.62 (65.54)	123.60 (41.48)
	ME	-2.35	-3.30	28.35	-3.28
Bodianus frenchii	RMSE	**22.49**	37.97 (68.80)	26.53 (17.94)	32.21 (43.22)
	ME	0.50	0.14	0.06	1.51
Epinephelides armatus	RMSE	**38.66**	44.29 (14.57)	62.06 (60.54)	42.90 (10.97)
	ME	2.26	0.11	5.84	0.37
Epinephelus coioides	RMSE	**55.97**	60.20 (7.57)	190.64 (240.61)	58.82 (5.09)
	ME	-0.37	-0.35	-23.09	-0.25
Glaucosoma hebraicum	RMSE	**62.67**	68.52 (9.30)	284.27 (353.47)	65.26 (4.11)
	ME	2.23	-0.83	-40.61	-0.85

Note. Bold font identifies the minimum RMSE for each species. BG = Bivariate Growth model; AEBPH = Age Effect Body Proportional Hypothesis; RIT = the re-arranged form of the regression equation used by Finstad (2003); AIT = the analogous form of the regression equation used by Finstad (2003).

Table 3*b*. Root Mean Square Error (RMSE) and mean error (ME) of otolith radius estimates for the bivariate growth model and for the Morita and Matshuishi (2001) and Finstad (2003) models calculated using ten-fold cross-validations for samples of 50 fish for each of *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides*, and *Glaucosoma hebraicum*. The percentages by which the RMSE of the alternative models differ from that of the bivariate growth model are presented in parentheses.

Species	Accuracy and precision measures	BG	AE	IT
Acanthopagrus butcheri	RMSE	**0.069**	0.070 (1.10)	0.072 (3.78)
	ME	0.003	< -0.001	0.001
Argyrosomus japonicus	RMSE	**0.484**	0.519 (7.28)	0.548 (13.19)
	ME	0.025	0.009	-0.035
Bodianus frenchii	RMSE	0.108	0.105 (-2.72)	**0.103 (-4.72)**
	ME	0.001	-0.001	< 0.001
Epinephelides armatus	RMSE	**0.095**	0.101 (6.61)	0.100 (4.99)
	ME	0.006	< 0.001	0.001
Epinephelus coioides	RMSE	0.097	0.106 (8.98)	**0.094 (-3.55)**
	ME	0.001	-0.001	0.001
Glaucosoma hebraicum	RMSE	**0.176**	0.199 (13.14)	0.191 (8.54)
	ME	0.004	-0.002	< 0.001

Note. Bold font identifies the minimum RMSE for each species. BG = Bivariate Growth model; AE = Age Effect model; IT = Interaction Term model.

Table 4*a*. Root Mean Square Error (RMSE) and mean error (ME) of total length estimates for the bivariate growth model and for models derived from the Morita and Matshuishi (2001) and Finstad (2003) models calculated using holdout and ten-fold cross-validations with and without the biological intercept for samples of *Acanthopagrus butcheri*. The percentages by which the RMSE of the alternative models differ from that of the bivariate growth model are presented in parentheses.

			Without the Biological Intercept				**With the Biological Intercept**			
Method	**Accuracy and precision measures**	**Number of fish**	**BG**	**AEBPH**	**RIT**	**AIT**	**BG**	**AEBPH**	**RIT**	**AIT**
Holdout validation	RMSE	N = 128	17.14	21.52	**16.84**	17.36	**17.34**	22.58	21.34	18.08
				(25.56)	(-1.72)	(1.28)		(30.22)	(23.05)	(4.27)
	ME		2.44	3.59	2.23	2.34	2.76	5.63	3.58	3.18
Ten-fold cross-validation	RMSE	N = 120	16.90	21.74	**16.84**	17.46	**16.79**	22.23	17.89	18.11
				(28.64)	(-0.37)	(3.34)		(32.43)	(6.52)	(7.85)
	ME		0.02	-0.39	-0.01	-0.03	0.03	1.03	1.31	1.08

Note. Bold font identifies the minimum RMSE for each species. BG = Bivariate Growth model; AEBPH = Age Effect Body Proportional Hypothesis; RIT = the re-arranged form of the regression equation used by Finstad (2003); AIT = the analogous form of the regression equation used by Finstad (2003). The holdout validation approach used 128 fish, 50 of which were employed when calculating the parameters of the models and 78 of which were held outside the fitting process for use in testing the accuracy and precision of model predictions. The ten-fold cross-validation involved the use of 120 fish, with each prediction based on a model fitted to data for 108 fish and predictions calculated for the other 12 fish on each pass through of the approach.

Table 4*b*. Root Mean Square Error (RMSE) and mean error (ME) of total length estimates for the bivariate growth model and the Morita and Matshuishi (2001) and the Finstad (2003) models calculated using holdout and ten-fold cross-validations with and without the biological intercept for samples of *Acanthopagrus butcheri*. The percentages by which the RMSE of the alternative models differ from that of the bivariate growth model are presented in parentheses.

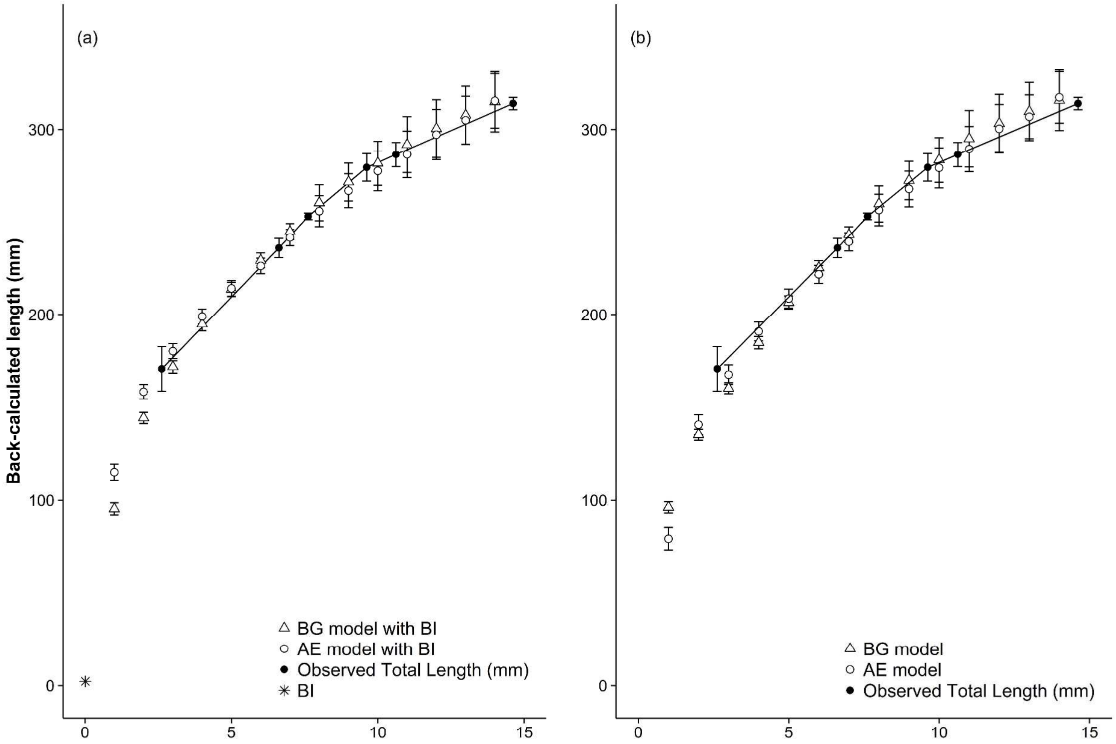
			Without the Biological Intercept			**With the Biological Intercept**		
Method	**Accuracy and precision measures**	**Number of fish**	**BG**	**AE**	**IT**	**BG**	**AE**	**IT**
Holdout validation	RMSE	N = 128	**0.070**	0.076	0.072	**0.071**	0.084	0.570
				(8.46)	(3.28)		(18.75)	(702.21)
	ME		-0.016	-0.019	-0.018	-0.016	-0.006	0.559
Ten-fold cross-validation	RMSE	N = 120	**0.070**	0.074	0.072	**0.070**	0.082	0.563
				(6.28)	(2.95)		(16.13)	(700.32)
	ME		0.002	-0.001	< -0.001	0.002	0.007	0.550

Note. Bold font identifies the minimum RMSE for each species. BG = Bivariate Growth model; AE = Age Effect model; IT = Interaction Term model. The holdout validation approach used 128 fish, 50 of which were employed when calculating the parameters of the models and 78 of which were held outside the fitting process for use in testing the accuracy and precision of model predictions. The ten-fold cross-validation involved the use of 120 fish, with each prediction based on a model fitted to data for 108 fish and predictions calculated for the other 12 fish on each pass through of the approach.

Table 5. Mean observed total length (mm) and mean age of fish within each age class in the 2013 sample of *Acanthopagrus butcheri*, together with mean back-calculated total lengths (mm) for fish at ages at zones bounding the age classes, calculated using different back-calculation approaches.

	Mean age of fish in age class at capture* and at zone (years)												
	2	**2.62***	**3**	**6**	**6.62***	**7**	**7.62***	**8**	**9**	**9.62***	**10**	**10.62***	**11**
Observed TL (mm)		170.80 (5.27)			236.00 (2.58)		253.15 (0.94)			279.50 (3.52)		286.50 (3.26)	
	Mean of back-calculated lengths for fish of different ages at zones												
BG model	136.43 (2.57)		161.32 (2.11)	**226.79** **(1.24)**		**244.16** **(0.83)**		**259.60** **(1.40)**	**272.01** **(1.78)**		**282.97** **(3.01)**		**295.01**
BG model with BI	**144.67** **(1.93)**		**173.23** **(2.78)**	**231.37** **(2.05)**		**246.77** **(1.29)**		**260.64** **(0.84)**	**271.65** **(1.08)**		**281.50** **(1.51)**		**291.84**
AE model	138.44 (3.51)		169.12 (5.95)	**227.00** **(3.79)**		**241.68** **(2.91)**		**256.83** **(2.91)**	267.60 (2.86)		**278.64** **(3.13)**		**289.41**
AE model with BI	**156.25** **(3.03)**		**181.27** **(4.29)**	**229.76** **(3.00)**		**243.43** **(2.65)**		**256.93** **(1.56)**	267.61 (1.72)		**277.52** **(0.46)**		**286.54**
IT model	140.20 (3.62)		169.57 (6.43)	**224.58** **(4.14)**		**238.43** **(4.13)**		**253.29** **(2.04)**	264.15 (2.86)		275.16 (1.77)		284.67
IT model with BI	**158.77** **(3.40)**		**182.38** **(4.90)**	**226.97** **(3.54)**		**239.44** **(4.35)**		252.23 (3.16)	262.99 (2.90)		272.46 (2.18)		279.06
MF model	145.36 (2.03)		168.54 (3.87)	221.81 (3.15)		235.98 (4.71)		248.97 (4.65)	262.00 (4.41)		271.55 (4.87)		277.82

Note. Standard errors are indicated between parentheses. Bold font indicates the range of back-calculated mean lengths at ages at zone between which mean observed total length (TL) falls for the corresponding age at capture (*). BI = biological intercept; BG = Bivariate Growth model; AE = Age Effect model described by Morita and Matsuishi (2001); IT = Interaction Term model described by Finstad (2003); MF = Modified Fry model described by Vigliola et al. (2000).


(a)
Back-calculated length (mm)
0
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200
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BG model with BI
AE model with BI
Observed Total Length (mm)
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(b)
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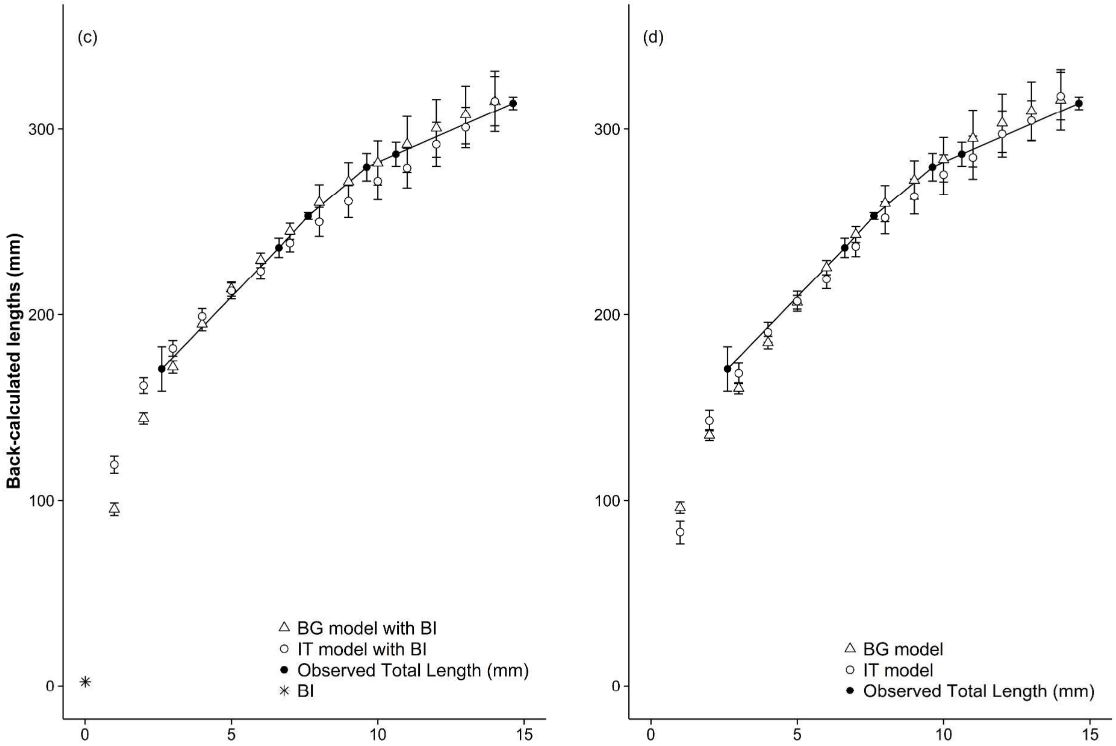
15
BG model
AE model
Observed Total Length (mm)

813


(c)
Back-calculated lengths (mm)
0
100
200
300
0
5
10
15
BG model with BI
IT model with BI
Observed Total Length (mm)
BI
(d)
0
100
200
300
0
5
10
15
BG model
IT model
Observed Total Length (mm)

814

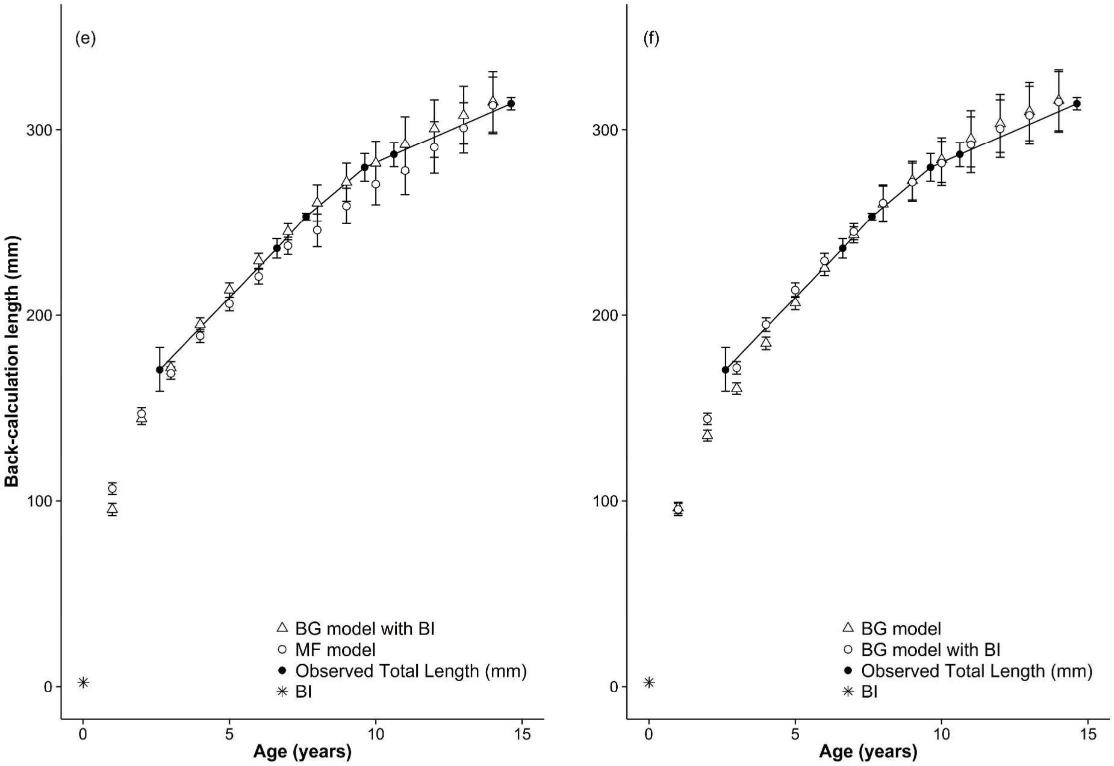


Figure 1. Comparison of mean observed total length (mm) versus mean age (years) of fish within each age class in the 2013 sample of *Acanthopagrus butcheri*, with the means of the total lengths (mm) at different ages at zones calculated using the different back-calculation approaches, i.e., the Bivariate Growth model (BG), the Age Effect model (AE) (i.e., the model described by Morita and Matsuishi (2001)), the Interaction Term model (IT) (i.e., model described by Finstad (2003)) and the Modified Fry model (MF) (i.e., model described by Vigliola et al. (2000)) with and without constraining the data through a biological intercept (BI) for *Acanthopagrus butcheri*. 95% confidence intervals are represented as error bars. Note that data for the single fish at 21 years of age was excluded.

Supplemental materials for Ashworth *et al.* CJFAS

Table S1. Maximum ages and total lengths (TL), sexuality, and habitats of *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides* and *Glaucosoma hebraicum*.

Species	Max. age (years)	Max. TL (mm)	Sexuality	Habitat	References
Acanthopagrus butcheri	31	530	Gonochorist	Temperate estuaries	Sarre and Potter (2000) Jenkins et al. (2006) Potter et al. (2008)
Argyrosomus japonicus	31	2000	Gonochorist	Coastal marine waters, seasonally entering estuaries	Farmer et al. (2005) Gomon et al. (2008)
Bodianus frenchii	78	480	Protogynous hermaphrodite	Over and around coastal temperate reefs	Gomon et al. (2008) Cossington et al. (2010) Platell et al. (2010)
Epinephelides armatus	19	510	Gonochorist	Over and around coastal temperate reefs	Moore et al. (2007) Gomon et al. (2008) Platell et al. (2010)
Epinephelus coioides	22	1110	Protogynous hermaphrodite	Subtropical/tropical mangrove nursery habitats and coastal reefs	Heemstra and Randall (1993) Heemstra (1995) Pember et al. (2005)
Glaucosoma hebraicum	41	1120	Gonochorist	Temperate coastal marine waters, around reefs	Hesp et al. (2002) Lenanton et al. (2009) Platell et al. (2010)

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Cossington, S., Hesp, S. A., Hall, N. G., and Potter, I. C. 2010. Growth and reproductive biology of the foxfish *Bodianus frenchii*, a very long-lived and monandric protogynous hermaphroditic labrid. J. Fish Biol. **77**(3): 600-626. doi: 10.1111/j.1095-8649.2010.02706.x.

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Table S2. Location and sampling regimes for *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides* and *Glaucosoma hebraicum* in estuarine and coastal waters along the western coast of Australia.

Species	Location	Method	References
Acanthopagrus butcheri	Wellstead Estuary (34°50'S, 118°60'E)	Seine and gill netting	Present study
Argyrosomus japonicus	Coastal waters between Carnarvon (24°53'S, 113°39'E) and Augusta (34°19'S, 115°10'E)	Gill netting Rod and line angling	Farmer et al. (2005)
Bodianus frenchii	Coastal marine waters along the lower west coast (between 30°18'S, 115°02'E and 32°30'S, 115°42'E)	Gill netting Rod and line angling Spear fishing	Cossington et al. (2010)
Epinephelides armatus	Coastal marine waters off the lower west coast of Australia (between 30°18'S, 115°02'E and 32°30'S, 115°42'E) (Murray Reef, Rottnest Island)	Fish traps Rod and line angling	Moore et al. (2007)
Epinephelus coioides	Kimberley and Pilbara coast (between 16°00'S, 126°00'E and 21°00'S, 119°00'E)	Fish traps Rod and line angling Trawl	Pember et al. (2005)
Glaucosoma hebraicum	Lower west coast of Australia between Mandurah (32°32'S) and the Houtman Abroholos (28°35'S)	Rod and line angling Spear fishing Trawl	Hesp et al. (2002)

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Cossington, S., Hesp, S. A., Hall, N. G., and Potter, I. C. 2010. Growth and reproductive biology of the foxfish *Bodianus frenchii*, a very long-lived and monandric protogynous hermaphroditic labrid. J. Fish Biol. **77**(3): 600-626. doi: 10.1111/j.1095-8649.2010.02706.x.

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