Age and growth rate variation influence the functional relationship between somatic and otolith size

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Age and growth rate variation influence the functional relationship between somatic and otolith size

Eloïse C. Ashworth\textsuperscript{a}, Norman G. Hall\textsuperscript{ab}, S. Alex Hesp\textsuperscript{b}, Peter G. Coulson\textsuperscript{a} and Ian C. Potter\textsuperscript{a}.

\textsuperscript{a}Centre for Fish and Fisheries Research, School of Veterinary and Life Sciences, Murdoch University, 90 South Street, Western Australia 6150, Australia.

\textsuperscript{b}Western Australian Fisheries and Marine Research Laboratories, Department of Fisheries, Post Office Box 20, North Beach, Western Australia 6920, Australia.

Corresponding author: eloise.c.ashworth@gmail.com
Abstract

Curves describing the length-otolith size relationships for juveniles and adults of six fish species with widely differing biological characteristics were fitted simultaneously to fish length and otolith size at age, assuming that deviations from those curves are correlated rather than independent. The trajectories of the somatic and otolith growth curves throughout life, which reflect changing ratios of somatic to otolith growth rates, varied markedly among species and resulted in differing trends in the relationships formed between fish and otolith size. Correlations between deviations from predicted values were always positive.

Dependence of length on otolith growth rate (i.e., ‘growth effect’) and ‘correlated errors in variables’ introduce bias into parameter estimates obtained from regressions describing the allometric relationships between fish lengths and otolith sizes. The approach taken in this study to describe somatic and otolith growth accounted for both of these effects and that of age to produce more reliable determinations of the length-otolith size relationships used for back-calculation and assumed when drawing inferences from sclerochronological studies.

Résumé

Les courbes décrivant les relations de longueur-taille de l’otolithe des juvéniles et adultes pour six espèces de poissons, aux caractéristiques biologiques très différentes, ont été ajustées simultanément à la longueur du poisson et à la taille de l’otolithe avec l’âge, en supposant que les déviations de ces courbes sont corrélées plutôt qu’indépendantes. Les trajectoires des courbes de croissance somatique et de l’otolithe tout au long de la vie, qui reflètent les changements de ratios des taux de croissance somatique et de l’otolithe, varièrent de façon marquée entre les espèces et aboutirent à des tendances distinctes dans les relations formées entre la taille des poissons et celle des otolithes. Les corrélations entre les déviations des valeurs estimées étaient toutes positives. La dépendance de la longueur du poisson sur le taux...
de croissance de l’otolithe (c’est-à-dire, l’effet de croissance) et les “erreurs corrélées dans les
variables” introduisent un biais dans les estimations de paramètres obtenues par les
régressions décrivant les relations allométriques entre les longueurs de poissons et les tailles
des otolithes. L’approche développée dans cette étude pour décrire la croissance somatique et
celle de l’otolithe tient compte de ces deux effets, ainsi que celui de l’âge, pour produire une
méthode plus fiable de détermination des relations de longueur-taille de l’otolithe, requises
dans les études de rétro-calcule et adoptées lors des conclusions tirées dans les études de
sclérochronologie.

**Keywords**

Somatic growth; otolith growth; length – otolith size relationship; correlated errors in
variables; bivariate distribution; age effect; growth effect.
Introduction

Data derived from the analysis of biological and environmental records preserved within the microstructure and chemistry of otoliths play a crucial role in the assessment and management of fish stocks, and in studies of their biology (e.g., Campana 1999, 2005; Begg et al. 2005). Thus, for example, since their inception, both the Alaska Fisheries Science Centre (AFSC) and the Centre for Environment, Fisheries and Aquaculture Science in the United Kingdom (CEFAS) have accumulated data for over a million otoliths (CEFAS 2014; Burke Museum 2015) and large numbers of these hard structures continue to be collected and processed each year by fisheries agencies worldwide to produce data for stock assessments (Campana and Thorrold 2001; Campana 2005). Studies of the effects of changes to fish habitat and environment on fish are of growing importance, particularly in view of the need to understand the implications of climate change. Because otoliths store information on inter-annual growth, these hard structures are being employed to explore the effects of variation in environmental factors on otolith growth (e.g., Pilling et al. 2007; Morrongiello et al. 2011; Coulson et al. 2014), and thereby draw inferences about how certain environmental factors influence somatic growth. Despite the value of the data derived from otoliths in such studies, however, it is somewhat surprising that the relationship between somatic and otolith growth remains poorly understood (Xiao 1996; Neuman et al. 2001; Fey and Hare 2012).

Otoliths are calcified structures used by fish for balance, hearing and orientation (e.g., Campana and Neilson 1985; Campana 1999; Popper et al. 2005). The growth of these structures, which vary widely in shape and size, is controlled by the combination of two processes: 1) the formation of an organic matrix, regulated by metabolic influences and, thus, to some extent linked to somatic growth; and 2) a physicochemical process, i.e., calcification (e.g., Gauldie and Nelson 1990a; Mugiya and Tanaka 1992; Campana 1999). Consequently,
if fish growth becomes negligible (e.g., hampered by starvation), otoliths continue to grow
due to the physiochemical and obligatory microincrementation processes involved in the
daily physiological cycle (e.g., Mosegaard et al. 1988; Gauldie and Nelson 1990b; Morales-
Nin 2000). These physiochemical processes also produce an ‘age effect’ in the relationship
between fish length and otolith size, where reduction in somatic growth as fish age is not
accompanied by a proportional change in otolith growth (e.g., Wright et al. 1990; Morita and
Matsuishi 2001; Vigliola and Meekan 2009).

Variation in rates of somatic growth for individuals of a species, i.e., a ‘growth rate
effect’, also influences otolith size and thus the relationship between fish length and otolith
size (Templeman and Squires 1956; Campana 1990; Somarakis et al. 1997). For example,
Secor and Dean (1989) found that larval and juvenile striped bass Morone saxatilis of a given
length from a pond in which slow somatic growth had been recorded had larger otoliths than
faster growing fish of the same size from a second pond in which faster somatic growth had
been recorded. In another study, Hare and Cowen (1995) found that larval and juvenile
bluefish Pomatomus saltatrix that were larger than the expected mean length at age possessed
otoliths larger than the size expected for fish of that age, and vice versa. These and other
studies (e.g., Strelcheck et al. 2003; Munday et al. 2004; Takasuka et al. 2008) indicate that,
because otolith growth is partially linked to metabolic processes, a positive, species-
dependent correlation is likely to exist between the deviations of length and otolith radius
from their expected sizes for fish of the same age, i.e., faster growing fish of a given age will
have faster growing otoliths. It appears likely that this correlation will be less for species
where the lengths at age of individuals approach their maximum sizes at relatively early ages,
than for species that continue to grow throughout life.

For a given population, the form of the length-otolith size relationship is a function of
the somatic and otolith growth curves (Hare and Cowen 1995). The forms of those growth
curves thus determine the manner in which the ratios of fish length to otolith radius, and rate of change of fish length to rate of change of otolith radius, vary with age. Because of the association of otolith growth with physiochemical as well as metabolic processes, growth of the otolith continues despite the decline in somatic growth as fish age, i.e., otolith growth becomes increasingly decoupled from somatic growth. As a consequence, the relative rates of predicted increase in fish length and otolith radius would be expected to decline with age, and, ultimately, given sufficient longevity, approach asymptotes of zero.

The overall objective of this study was to test the above hypotheses using data for juveniles and adults of six fish species, which belong to different families, possess widely varying biological characteristics and occupy a range of environments. Thus, for each species, a model was fitted to describe somatic and otolith growth and to determine the bivariate distribution of the deviations of the lengths and otolith radii at age from those curves. For each species, the correlation of the resulting bivariate distribution of deviations was then tested to determine whether, as hypothesised, it was positive and significantly greater than zero. Trends in the predicted relative rates of somatic and otolith growth with age were examined to determine whether, as expected, these declined with age. The implications of the findings for back-calculation and sclerochronological studies are discussed.

**Materials and Methods**

**1.1 The six selected species**

The six species selected for this study were Black Bream, *Acanthopagrus butcheri* (Munro 1949); Mulloway, *Argyrosomus japonicus* (Temminck and Schlegel 1843); Foxfish *Bodianus frenchii* (Klunzinger 1880); Breaksea Cod *Epinephelides armatus* (Castelnau 1875); Goldspotted Rockcod *Epinephelus coioides* (Hamilton-Buchanan 1822) and West...
Australian Dhufish *Glaucosoma hebraicum* Richardson, 1845. Maximum ages and lengths for these temperate and subtropical species ranged from ~19 to 78 years and from ~480 to 2000 mm, respectively\(^1\).

The data for *A. butcheri* were derived from samples collected during the present study\(^2\), whereas those for each of the other species were derived using samples collected in previous studies in Western Australia by staff and research students at Murdoch University. The methods employed and locations from which individuals of each species were collected, are listed in supplemental materials\(^3\). Details of the sampling regimes for *A. japonicus*, *B. frenchii*, *E. armatus*, *E. coioides*, and *G. hebraicum* are provided in the associated references describing those respective studies\(^3\).

This study was conducted in accordance with conditions in permit R2561/13 issued by the Murdoch University Animal Ethics Committee.

**1.2 Fish processing and otolith measurements**

The total length (TL) of each *A. butcheri* was measured to the nearest 1 mm and its two sagittal otoliths removed and stored. The left sagittal otolith of each of 50 randomly-selected individuals was embedded in clear epoxy resin and, using an Isomet\(^\circledR\) low-speed saw (Buehler Ltd., Lake Bluff, Illinois), cut transversely into ~0.3 mm sections through its primordium and perpendicular to the sulcus acusticus. The sections were cleaned, polished with wet and dry carborundum paper (grade 1 200) using tap water, dried and mounted on microscope slides under coverslips using DePX mounting adhesive. Essentially the same procedure had been employed to prepare the otolith sections of the other five species, although for several species (i.e., *A. japonicus*, *E. coioides* and *G. hebraicum*), the sections

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\(^1\) for further details of these species, see Table S1  
\(^2\) Supplemental material S1  
\(^3\) Table S2
were not polished. For each of these species, 50 otolith sections were randomly selected for
the current study, noting that a common sample size was employed to facilitate comparability
among species.

Otolith sections for individuals of all species were examined under reflected light against
a black background using a high-resolution digital microscope camera (Leica DFC 425) with
5 Mpixel resolution mounted on a dissecting microscope (Leica MZ7.5) with a magnification
range of 6.3x to 50x. High-contrast digital images of the sectioned otoliths were analysed
using the computer imaging package Leica Application Suite version 3.6.0 (Leica
Microsystems Ltd 2001).

The opaque zones in each sectioned otolith for *A. butcheri* were counted independently
and on different occasions by E. Ashworth and P. Coulson, without knowledge of the size of
the fish. On the few occasions when the counts of these two readers disagreed (< 2%), the
two readers discussed the basis for the discrepancy and determined a mutually agreed value.
As for the other five fish species, the age of each *A. butcheri* was determined using the
number of opaque zones in its otoliths, its date of capture and the assumed birth date (i.e., the
approximate mid-point of the spawning season)\(^4\) and knowledge of when the new opaque
zone becomes delineated from the otolith periphery for that species. The ages assigned in
earlier studies to the individuals of the other species were accepted for use in the current
study. For all six species, opaque zones have been shown to be formed annually in their
otoliths.

For each species, the ‘radius’ of each otolith, i.e., the distance between the primordium
and the outer edge of the otolith, was measured on three occasions to the nearest 0.1 µm
along a line perpendicular to the opaque zones along the posterior edge of the sulcus of the
otolith using digital images of the sectioned otoliths, taken under reflective light. The mean of

\(^4\) Table S3
these three measurements for each otolith was used as the radius of that otolith in subsequent analyses.

1.3 Analyses

1.3.1 The bivariate model used to describe somatic and otolith growth

Total fish length, $L$, and otolith radius, $R$, were each assumed to grow in accordance with a growth curve of the form,

$$g_S(t | S_{r_1}, S_{r_2}, a_S, b_S),$$

which describes size $S$ (either $L$ or $R$) as a function of age $t$, where $S_{r_1}$ and $S_{r_2}$ are the expected sizes at two specified reference ages $\tau_1$ and $\tau_2$, 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 $\tau_1$ and $\tau_2$ in this study. Thus, the expected length $\hat{L}_j$ of fish $j$ at its age at capture $t_{c,j}$ was calculated as

$$\hat{L}_j = g_L(t_{c,j} | L_{r_1}, L_{r_2}, a_L, b_L)$$

and the radius of its otolith as $\hat{R}_j = g_R(t_{c,j} | R_{r_1}, R_{r_2}, a_R, b_R)$.

The expected size at age $t$, was calculated using either a modified version of the von Bertalanffy growth equation that allowed for an oblique linear asymptote or the versatile growth model described by Schnute (1981). The modified von Bertalanffy equation is:

$$S(t) = g_S(t | S_{r_1}, S_{r_2}, a_S, b_S) = c[1 - \exp[-a_s(t - b_s)]] + d(t - b_s),$$

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 following four equations comprise the Schnute (1981) model:

\[
S(t) = g_S(t | S_{r_1}, S_{r_2}, a_S, b_S) = \begin{cases} 
S_{r_1} \exp \left[ \ln \left( \frac{S_{r_2}}{S_{r_1}} \right) \left( \frac{1 - e^{-a(t - \tau_1)}}{1 - e^{-a(\tau_2 - \tau_1)}} \right) \right] & \text{if } a_S \neq 0, b_S \neq 0 \\
\left[ S_{r_1} + (S_{r_2} - S_{r_1}) \frac{1 - e^{-a(t - \tau_1)}}{1 - e^{-a(\tau_2 - \tau_1)}} \right]^{b-1} & \text{if } a_S \neq 0, b_S = 0 \\
\left[ S_{r_1} + (S_{r_2} - S_{r_1}) \frac{t - \tau_1}{\tau_2 - \tau_1} \right]^{b-1} & \text{if } a_S = 0, b_S \neq 0 \\
S_{r_1} \exp \left[ \ln \left( \frac{S_{r_2}}{S_{r_1}} \right) \left( \frac{t - \tau_1}{\tau_2 - \tau_1} \right) \right] & \text{if } a_S = 0, b_S = 0 
\end{cases}
\]

Sixteen alternative growth models were considered. These comprised the modified von Bertalanffy curve and 15 alternative forms of the Schnute (1981) growth curve, each of which was formed by constraining \(a_S\) and \(b_S\) to specific values or ranges and thereby ensuring that no discontinuity was present in the derivatives of the negative log-likelihood in the ranges over which, for that model, those two parameters extended. These alternative model forms included many of the growth curves commonly used in fisheries science, e.g., von Bertalanffy, Richards, Gompertz, etc. (Schnute 1981)\(^5\).

Deviations of total length, \(L\), and otolith radius, \(R\), for fish of age \(t\) years about the length \(\hat{L}\) and radius \(\hat{R}\) predicted by the growth curves for these variables were assumed to be drawn from one of four candidate bivariate distributions. Thus, for each analysis, for fish \(j\) at its age of capture \(t_{c,j}\), the deviations of its recorded values of length \(L_j\) and otolith radius \(R_j\) from the expected values for fish of that age were drawn from either the bivariate normal, normal-lognormal, lognormal-normal, or bivariate lognormal distributions. The form of this distribution determines the forms of the associated marginal distributions for the deviations of lengths and otolith radii from their expected values. That is, the recorded length \(L_j\) and otolith

\(^5\) Supplemental material S2 and Table S4
radius $R_j$ of fish $j$ at its age at capture $t_{c,j}$ around their respective expected values at that age, i.e., $\hat{L}_j$ and $\hat{R}_j$, were drawn from either normal distributions, i.e., $L_j = \hat{L}_j + \epsilon_j$ or $R_j = \hat{R}_j + \eta_j$, or lognormal distributions, i.e., $L_j = \hat{L}_j \exp(\epsilon_j)$ or $R_j = \hat{R}_j \exp(\eta_j)$, where, in each case, the correlation between values of $\epsilon$ and $\eta$ is $\rho$.

Specifically, the study considered the following candidate bivariate distributions when fitting growth models to recorded lengths and otolith radii of fish at their different ages of capture:

1. a bivariate normal distribution, where

$$ (L_j, R_j) \sim \text{BVN}(\hat{L}_j, \hat{R}_j, \sigma^2_\epsilon, \sigma^2_\eta, \rho), $$

2. a bivariate normal (fish length) – lognormal (otolith radius) distribution, where

$$ (L_j, R_j) \sim \text{NLN}(\ln(\hat{L}_j) - \sigma^2_\epsilon/2, \hat{R}_j, \sigma^2_\eta, \rho), $$

3. a bivariate lognormal (fish length) – normal (otolith radius) distribution, where

$$ (L_j, R_j) \sim \text{LNN}(\ln(\hat{L}_j) - \sigma^2_\epsilon/2, \hat{R}_j, \sigma^2_\eta, \rho), $$

4. a bivariate lognormal distribution, where

$$ (L_j, R_j) \sim \text{BVLN}(\ln(\hat{L}_j) - \sigma^2_\epsilon/2, \ln(\hat{R}_j) - \sigma^2_\eta/2, \sigma^2_\eta, \rho), $$

and where the probability density functions for these distributions are presented in the supplemental materials. As shown above, the means of log-transformed values in the above distributions were assumed to be offset from zero by $-\sigma^2/2$ to ensure that the expected values of $L_j = \hat{L}_j \exp(\epsilon_j)$ or $R_j = \hat{R}_j \exp(\eta_j)$ are $\hat{L}_j$ or $\hat{R}_j$, respectively.

A phased approach, which entailed first exploring the forms of growth models and statistical distributions that best described somatic and otolith growth, facilitated fitting of the full bivariate model by providing initial estimates of parameters and identifying the structural forms of the two growth models and their associated marginal distributions to be employed in

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6 Supplemental material S3
that final model. Akaike Information Criterion corrected for small sample sizes (AICc; Akaike 1974; Hurvich and Tsai 1989; Anderson and Burnham 2002) and Akaike Weight (AW; Burnham and Anderson 2002; Katsanevakis and Maravelias 2008) were calculated to determine the models and statistical distributions that best described the lengths at age and otolith sizes at age. The fitted model that produced the minimum value of AICc, and thus the greatest value of AW, was selected as providing the best description of fish lengths or otolith radii at ages at capture. Models with AICc scores that differ by less than ~ 2 from that of the model with the lowest AICc are strongly supported by the data and provide representations of the data of almost similar quality to that provided by the model with the lowest AICc (Anderson and Burnham 2002; Okamura and Semba 2009).

Models were developed in Template Model Builder (package ‘TMB’, Kristensen 2015), in combination with the function ‘nlminb’, within R (R Development Core Team 2011). Thus, for each of the four alternative bivariate distributions and for each pair (i.e., somatic and otolith) of the 16 alternative growth models, the parameters that minimised the negative log-likelihood, \( \lambda_{L\text{otolith}} \), of the deviations of the pair of lengths and otolith radii at their ages of capture from their expected values given the bivariate distribution of those deviations were calculated. Note that the equations for the negative log-likelihoods of the bivariate distributions scale the variables appropriately, thereby accounting for their very different magnitudes.\(^7\)

The parameters estimated for each bivariate model were those for the somatic growth equation, i.e., \( L_{T_1}, L_{T_2}, a_L, b_L, \) and \( s_e \), those for the otolith growth equation, i.e., \( R_{T_1}, R_{T_2}, a_R, b_R, \) and \( s_\eta \), and the correlation \( \rho \) of the bivariate distribution. Note also that \( s_e \) and \( s_\eta \) are estimates of the standard deviations \( \sigma_e \) and \( \sigma_\eta \), respectively, and that an appropriate subset of parameters was estimated when one or more of the shape parameters of the Schnute (1981)

\(^7\) Supplemental material S3
model(s) was set to zero or to specific fixed values for particular forms of this curve. Values of the adjusted coefficient of determination, $R^2_{\text{adjusted}}$, were calculated for the fits provided to lengths and otolith sizes at age by the somatic and otolith growth curves, respectively, of the fitted bivariate growth model.

To provide further information on the form of the model (and associated statistical distribution of deviations from that model) that best described the lengths and otolith radii at age for each species, a bootstrapping analysis was undertaken by resampling 4,000 random data sets, with replacement, from the observed data for each species. For each random data set, the bivariate model was fitted and the resulting parameter estimates were stored. The proportions of bootstrap results that resulted in the selection of each model form were calculated.

1.3.2 Correlation between deviations from somatic and otolith growth

The proportion of the 4,000 bootstrap estimates of correlation that were less than or equal to zero for each species was calculated. A one-tailed t-test, calculated using the estimated standard error (SE) produced as output by TMB when fitting the model, was used to determine whether the correlation for each species was significantly greater than zero (i.e., $P < 0.05$).

1.3.3 Relationship between expected length and expected otolith radius

The expected lengths and otolith radii were calculated for ages extending over the observed range of ages for each species. The relationship formed by plotting the resulting expected lengths at age against associated otolith radii at age for each species was compared with the recorded fish lengths and otolith radii. To aid this exploration, instantaneous rates of somatic and otolith growth at each age within the age range for each species were calculated from the fitted curves using a forward difference approximation of the derivative (e.g.,
To adjust for the different magnitudes of the two variables, instantaneous relative rates of somatic and otolith growth at each age were then calculated by dividing the instantaneous rates by predicted length and otolith radius at age respectively.

**Results**

**Forms of growth curves providing best descriptions of length at age**

The curves that best described the lengths at ages of capture of the sampled fish in the bivariate growth models fitted to the length and otolith data for the different species varied considerably (Table 1; Fig. 1). The somatic growth curves identified as best representing lengths at age included the Pütter number 2 growth curve for *A. butcheri*, the traditional von Bertalanffy curve for both *A. japonicus* and *E. coioides*, the modified von Bertalanffy curve (i.e., with oblique linear asymptote) for *B. frenchii*, a logistic model for *E. armatus*, and a Schnute (1981) model with parameters $a = 0$ and $b > 0$ for *G. hebraicum*.

For five of the six species, the same somatic growth curves were identified using AICc and the bootstrapping procedure (Table 2). In the case of *A. butcheri*, however, the traditional von Bertalanffy model was most frequently (36% of samples) identified as the most appropriate somatic growth curve. It should be noted that, for *A. japonicus*, the modified von Bertalanffy curve provided the best representation of lengths at age of the bootstrapped samples almost as frequently as the traditional von Bertalanffy curve, differing by only 0.3%.

For four of the six species (i.e., except *E. armatus* and *G. hebraicum*), the AICc scores calculated for several alternative somatic growth curves when fitting the bivariate growth model to the observed length and otolith data were only slightly greater (differing by $< 2$ units) than the AICc of the selected model. For *A. butcheri*, the AICc scores of the

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8 Table S5
9 Table S6
traditional von Bertalanffy, Gompertz curve and logistic curves, all with normally distributed
deviations, lay close to and within 2 units of that of the Pütter number 2 curve\textsuperscript{10}. For
\textit{A. japonicus} and \textit{E. coioides}, the AICc scores of the Pütter number 2 curve approached those
(and within 2 units) of the traditional von Bertalanffy curves. The modified von Bertalanffy
curve, with the lognormal distribution, provided a description of the lengths at age of
\textit{B. frenchii} that was of similar quality (and with an AICc that differed by < 2 units) to that
produced by the same curve with normally-distributed deviations. The quantitatively similar
lengths at age predicted for the different species by those somatic growth curves with AICc
scores exceeding those of the best models by < 2 units differed only slightly from the values
calculated using those latter models, with differences most evident at the ends of the age
ranges or, within those ranges, where data were sparse\textsuperscript{11}.

\textbf{Forms of growth curves providing best descriptions of otolith radius at age}

The curves that were identified as best describing otolith growth when fitting the
bivariate growth model showed greater consistency among the different species than those
that described somatic growth (Table 1). Schnute (1981) growth curves with parameters $a = 0$
and $b > 0$, which have no inflection point or finite asymptote, best represented the otolith
sizes at age for \textit{A. butcheri}, \textit{A. japonicus}, and \textit{B. frenchii} (Table 1; Fig. 2; Tables S7 and S8).
The traditional von Bertalanffy growth curve best represented otolith sizes within the age
range of the sample for both \textit{E. armatus} and \textit{E. coioides}. For the former species, the rate of
growth slowed markedly by $\sim$ 7 years of age, whereas in the case of \textit{E. coioides}, the radii of
its otoliths continued to increase in size without slowing markedly as they approached the
upper end of their age range. Finally, otolith sizes at age for \textit{G. hebraicum} were best
described by the modified von Bertalanffy model, where, following rapid growth until

\textsuperscript{10} Table S6
\textsuperscript{11} Fig. S1
~ 4 years of age, the radii continued to increase, approximately linearly, with age over the
remainder of the age range of the sample. The same growth curves were identified using
AICc and the bootstrapping procedure (Table 2).

For *B. frenchii*, the modified von Bertalanffy and a Schnute (1981) curve with \( a < 0 \)
and \( b > 0 \) differed by less than 2 units from the AICc best model\(^{12}\). The AICc scores of the
Püttter number 2, the Gompertz, a Schnute (1981) curve with \( a = 0 \) and \( b > 0 \), the logistic, and
the modified von Bertalanffy curves describing otolith size at age of *E. armatus* were similar
to the traditional von Bertalanffy curve identified as best representing those otolith sizes at
age. For *E. coioides*, the AICc scores of the Schnute (1981) curve with \( a = 0 \) and \( b > 0 \), the
modified and the generalised von Bertalanffy curves were within 2 units of the traditional von
Bertalanffy curve. A Schnute (1981) model with parameters \( a < 0 \) and \( b > 0 \) provided another
alternative model with a quantitatively similar description of otolith growth for *G. hebraicum*.

As with the somatic growth curves, differences for each species between the otolith radii at
age predicted by the models with AICc scores exceeding that of the best model by < 2 units
and the values predicted by that latter model differed only slightly and mainly at the ends of
the age range or, within that range, where data were sparse\(^{13}\).

**Distribution of lengths and otolith radii at age about growth curves**

The somatic growth curves for *A. butcheri*, *A. japonicus*, *B. frenchii* and *E. coioides*
that employed a normal rather than lognormal marginal distribution provided the best
description of the deviations of observed lengths at age from the values predicted by the
growth curve (Table 1). For both *E. armatus* and *G. hebraicum*, however, lognormal
distributions were the best.

\(^{12}\) Table S8
\(^{13}\) Fig. S2
Lognormal distributions provided the most appropriate descriptions of the deviations from the otolith growth curves for five of the six species, with the exception being *E. coioides*, for which the marginal distribution of the deviations was best represented by the normal distribution (Table 1).

*Descriptions of somatic growth provided by the fitted bivariate growth models*

The quality of the fit to lengths at age provided by the bivariate growth model was high for five of the six species (i.e., $R^2_{\text{adjusted}} > 0.88$), with *E. armatus* being the exception, for which $R^2_{\text{adjusted}}$ was 0.79 (Table 3; Fig. 1). The lengths at age of individuals of *A. butcheri* and *A. japonicus* predicted by the somatic growth curves of the fitted bivariate models approached horizontal asymptotes as age increased, whereas those of individuals of *B. frenchii, E. armatus, E. coioides* and *G. hebraicum* continued to increase throughout the range of observed ages (Fig. 1). In contrast to *E. armatus, E. coioides* and *G. hebraicum*, for which the rates at which predicted lengths at age were positive but continued to slow with age, those for *B. frenchii* approached an oblique linear asymptote. The total lengths at age for younger *A. japonicus* and *B. frenchii*, (i.e., fish with ages $< \sim 8$ and $\sim 10$ years, respectively) increased rapidly but individuals of these species then exhibited much slower growth over the remainder of their lives (Figs 1b and c), noting that, in samples used in this study, these two species had the greatest maximum ages, i.e., $\sim 30$ years for *A. japonicus* and $\sim 61$ years for *B. frenchii*. In the case of *E. armatus*, the curve describing the lengths at age exhibited a slightly sigmoid shape with an apparent point of inflection at an age of 3.9 years (Fig. 1d).

*Descriptions of otolith growth provided by the fitted bivariate growth models*

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14 Table S9
For the five species for which $R^2_{\text{adjusted}}$ of lengths at age were high, similarly high quality fits to otolith radii at age were produced by the fitted bivariate growth models (i.e., $R^2_{\text{adjusted}} > 0.87$). As with its somatic growth curve, a poorer fit ($R^2_{\text{adjusted}} = 0.53$) of otolith sizes at ages was obtained for *E. armatus* (Table 3; Fig. 2).

Values of otolith radii predicted using the fitted growth curves for *A. butcheri*, *A. japonicus*, *B. frenchii*, *E. coioides* and *G. hebraicum* continued to increase markedly with ages of capture throughout the age ranges of the different species (Fig. 2). For *E. armatus*, however, the rate of growth of the otolith radii slowed more appreciably as the expected values of the radii appeared to approach an asymptote at a relatively early age within the range of ages, and thus, by age $\sim 4$ years, the radii had attained 76% of their predicted asymptotic size. The initial rapid rate of growth of the otolith radii of *G. hebraicum*, i.e., 1.20 mm.year$^{-1}$ at $\sim 2$ years, was reduced from age $\sim 5$ years to a much lower but more constant rate of growth, i.e., 0.1 mm.year$^{-1}$.

### Correlations between deviations from somatic and otolith growth curves

The maximum likelihood estimates of the correlations of the bivariate distributions of deviations from the fitted somatic and otolith growth curves were positive for all species, although the values of correlations estimated for some bootstrap trials, and particularly those of *B. frenchii*, fell below zero (Table 4). Although results of the one-tailed t-test demonstrated that the point estimates of the correlation were significantly greater than zero for *A. butcheri* ($P < 0.05$), *E. coioides* ($P < 0.001$), and *G. hebraicum* ($P < 0.001$), this was not the case for *A. japonicus*, *B. frenchii* and *E. armatus* (all $P > 0.05$). The correlations of the bivariate distributions of deviations from lengths and otolith radii at age predicted for the different species by those somatic and otolith growth curves with AICc scores exceeding those of the

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$^{15}$ Table S9
best models by < 2 units were all positive and the one-tailed test demonstrated that the point estimates of the correlations for these quantitatively similar bivariate models were significantly greater than zero for *E. coioides* (*P* < 0.001) and *G. hebraicum* (*P* < 0.001).\(^{16}\)

**Relationships between expected total fish lengths and otolith sizes at age**

The curves relating the expected values of total length to otolith radius for five of the six species, i.e., *A. butcheri*, *A. japonicus*, *B. frenchii*, *E. coioides* and *G. hebraicum*, appeared to match the trends exhibited by the observed total lengths and otolith radii at capture (Fig. 3). The curve formed by the predicted values for *E. armatus* provided a poor representation of the rather unusual ‘sigmoid’ pattern exhibited by the observed lengths and otolith radii at age of the individuals for this species (Fig. 3d).

The expected lengths at age of *A. japonicus* increased approximately linearly with the associated expected sizes of their otoliths for smaller otoliths but then approached a well-defined asymptotic length as otolith sizes continued to increase (Fig. 3b). A similar slowing of the rate of increase in expected length relative to expected otolith radius as the latter increased towards their maxima was apparent for both *A. butcheri* and *G. hebraicum*, but the lengths at age of the latter species had not approached an asymptote (Figs 3a and f). There appeared to be no similar decline in the rates at which predicted lengths at age increased relative to expected otolith sizes as the latter increased towards their maxima for *B. frenchii*, *E. armatus*, and *E. coioides* (Figs 3c, d, and e). The relationship between predicted length and otolith size at age for *G. hebraicum* displayed an obvious point of inflection at an otolith radius of ~ 2 mm (Fig. 3f). Similar, but less obvious inflection appeared present in the length-otolith radius relationships for *A. butcheri* and *A. japonicus* (Figs 3a and b). Throughout the ranges of their otolith sizes, the relationships between expected length and associated

\(^{16}\) Table S10
expected otolith size for both *E. armatus* and *E. coioides* displayed increasing trends (Figs 3d and e).

The alternative curves for each species, which related the predicted lengths and otolith radii at the same age for different combinations of the somatic and otolith growth curves that lay within 2 AICc units of the AICc of the best fitting curves, were quantitatively similar to that produced by the fitted bivariate growth model, with slight differences at the ends of the ranges of lengths and otolith radii or, within those ranges, where data were sparse\(^\text{17}\).

For all six species, predicted relative instantaneous rates of somatic and otolith growth declined with age towards zero (Fig. 4). In the case of *A. butcheri*, the relative rate of otolith growth was initially greater than that of somatic growth (Fig. 4a). It subsequently declined slightly more rapidly, being overtaken at an age of ~ 6 years by the declining relative rate of somatic growth. The relative rate of otolith growth slowed to become almost constant, but non-zero, at older ages within the range of observed ages, while that of somatic growth appeared to approach an asymptote of zero. The initial relative rate of otolith growth for *A. japonicus* was also greater than that of somatic growth, but both exhibited a very rapid and similar marked decline towards much reduced levels (Fig. 4b). For the remainder of the observed age range, the relative rates of growth for this species remained approximately constant with that for otolith growth remaining at a slightly greater level than that for somatic growth, which became close to zero for ages > ~ 10 years. For *B. frenchii*, the initial relative rate of somatic growth greatly exceeded that of otolith growth, but declined rapidly to fall below the latter at an age of ~ 5 years, approaching an apparent asymptote of zero (Fig. 4c).

From the age when the relative otolith growth rate overtook the relative rate of somatic growth, it remained above but gradually declined towards that latter growth rate through subsequent ages of the observed age range.

\(^{17}\) Fig. S3
For *E. armatus*, the initial relative rate of otolith growth was greater than that of somatic growth and, within the observed age range, declined far more rapidly than the latter towards an apparent asymptote of zero (Fig. 4d). Although differing in magnitude and rate, this decline had a similar form to that of the other five species. In contrast, however, the instantaneous relative rate of somatic growth of this species declined approximately linearly until an age of ~ 8 years, before the rate of decline began to slow as ages approached their maximum. The relative rate of somatic growth of *E. armatus* exceeded that for otolith growth over virtually all of its observed age range.

As with *B. frenchii*, the initial relative rate of somatic growth for *E. coioides* greatly exceeded that of its otolith growth (Fig. 3.4e). Both growth rates declined towards an apparent asymptote of zero with age, with the somatic growth rate remaining greater than the otolith growth rate throughout the entire observed age range. For *G. hebraicum*, the relative rate of otolith growth declined rapidly from its initial level, which was only slightly less than that of somatic growth, to become markedly less than that rate of growth by the age of ~ 3 years (Fig. 4f). Both curves appeared to decline towards a zero asymptote.

**Discussion**

The inclusion of age improves the precision of the estimated relationship between fish length and otolith size for back-calculation (e.g., Francis 1990; Kielbassa et al. 2011). Thus, for example, Sirois et al. (1998) extended the ‘biological intercept’ method of calculation proposed by Campana (1990) to include age, while Morita and Matsuishi (2001) modified the linear relationship between otolith size and fish length to incorporate this variable. The latter model was further extended by Finstad (2003), who added an interaction term. Xiao (1996) coupled somatic growth curves (von Bertalanffy, logistic, and Gompertz) with an allometric relationship between otolith size and fish length, assuming constant allometric parameters, to
form equations relating otolith size to fish length. To the best of our knowledge, however, the current study is the first to fit growth curves to lengths and otolith radii at ages of capture for juveniles and adults of different species, to explore the forms of those curves that best describe the otolith data, and to use predictions from those fitted curves over the range of observed ages to relate expected fish length at any given age to expected otolith radius at that age. It is noted, however, that Hare and Cowen (1995) fitted first to fourth-order polynomials to explore relationships between length, otolith radius and age for larvae and juveniles of *Pomatomus saltatrix*.

The inclusion of age as an explanatory variable in the equation relating fish length to otolith radius accounts directly for the ‘age effect’, in which otolith size continues to increase when somatic growth is little or null (e.g., Mugiya 1990; Secor and Dean 1992; Morita and Matsuishi 2001). By recognising the bivariate distribution of the deviations of fish lengths and otolith radii from the expected lengths and radii of the individual fish at their ages at capture, the bivariate model has also taken the ‘growth effect’ into account. This effect, which results from the relationship between the size of the otolith of an individual fish and its rate of somatic growth, is exemplified by the fact that slow-growing fish have larger otoliths than faster growing fish of the same size (e.g., Reznick et al. 1989; Campana 1990). Correlation between deviations from the somatic and otolith growth curves converts an ‘errors in variables’ issue, commonly encountered in allometric relationships such as that between length and otolith radius (Laws and Archie 1981; Xiao 1996; Katsanevakis et al. 2007), into a ‘correlated errors in variables’ problem, adding to the statistical issues encountered when fitting equations to describe the relationship (Fuller 1980; Thoresen and Laake 2007). The bivariate growth model developed for this study takes such individual variation and potential for correlation of deviations into account, thereby directly addressing this issue.
Growth

The analyses demonstrated that the bivariate growth model provided good fits ($R^2_{\text{adjusted}} > 0.87$) to the lengths and otolith sizes at age of the individuals of five of the six teleost species considered in this study. As these species had different biological characteristics, it was expected that the functional forms of the growth curves and the error distributions would differ among the species.

Somatic growth

The von Bertalanffy growth curve had been employed in the earlier studies of *A. japonicus*, *B. frenchii*, *E. armatus*, *E. coioides* and *G. hebraicum*, from which the samples for the current study were drawn, and in earlier studies for *A. butcheri*\(^{18}\). In the current study, however, only the lengths at age for *A. japonicus* and *E. coioides* were described best by such a curve.

In theory, because energy is directed towards reproduction and cell maintenance rather than somatic growth as fish approach maturity and continue to age, length is expected to approach an asymptote as age increases (Charnov et al. 2001; West et al. 2001; Lester et al. 2004). While the forms of Schnute (1981) growth curves that best described lengths at age for four of the six species in this study possessed a finite (horizontal) asymptote, the fitted somatic growth curves for *B. frenchii* (i.e., a modified von Bertalanffy curve) and *G. hebraicum* (i.e., a Schnute (1981) curve with $a = 0$ and $b > 0$) did not. It is possible that, for these two species, the samples possessed few individuals of sufficient age to facilitate selection of a form of model that included a finite asymptote. For example, the age range for *G. hebraicum* was 0.7 to 24.2 years in this study, yet its maximum recorded age is 41 years (Hesp et al. 2002). Although the ages of *B. frenchii* employed in this study, i.e., 1.1 to

\(^{18}\) for references to previous studies, see Table S2
61.9 years, provided better coverage of the expected age range (noting that the maximum age
of this species is 78 years), few fish within the sample had ages in excess of 42 years
(Cossington et al. 2010).

For two of the six species, the growth curves identified as best representing lengths at age
possessed points of inflection (at 0.69 years for *A. butcheri* and at 3.9 years for *E. armatus*).
The ages associated with these points of inflection are only slightly greater than the minimum
ages of the fish in the samples. Although it is possible that the fitted curves reflect the
acceleration of fish growth at young ages, and the subsequent decline in rate of growth at
older ages (Campana and Jones 1992), the paucity of young fish in the samples for these two
species may have influenced the forms of the somatic growth curves fitted to the data (e.g.,

The recommendation of Katsanevakis and Maravelias (2008) that, when fitting growth
models, it is appropriate to explore the form of curve that best describes the size at age, is
supported by the different forms of growth curves that were identified as providing the best
representations of the data for the six species considered in the current study.

**Otolith growth**

The analyses showed that the patterns for otolith growth were more consistent among
the studied species than those for somatic growth for those species, with otoliths of
individuals of all but *E. armatus* exhibiting continued marked growth over the range of
observed ages. This finding is in accordance with the concept that, although somatic growth
decreases with age, deposition of material on the surface of the otolith continues to occur
with the rate of deposition varying in response to the different exogenous factors (e.g.,
temperature) involved (e.g., Bradford and Geen 1992; Morales-Nin 2000; Fey 2006). Indeed,
for *A. butcheri, A. japonicus, B. frenchii* and *G. hebraicum*, the annual increment in otolith
radius had become almost constant with age over the range of observed ages. Although the form of the fitted growth curve for *E. coioides*, i.e., a traditional von Bertalanffy curve, suggested that otolith radius was approaching an asymptote as age increased, the predicted annual increment still remained well above 0 mm/year\(^1\) for fish of the maximum observed age. In contrast to the other five species, the otolith radii for older individuals of *E. armatus* appeared to have closely approached their asymptotic size.

There would be value in investigating whether growth in otolith mass or distances along other axes of measurement produce otolith growth curves that, although possibly of different forms, are consistent with those obtained using the axis of measurement employed in this study. In such a future study, there would also be value in collecting samples containing greater numbers of older individuals to assess whether, over a broader range of ages, the otoliths of older individuals of the different species continue to grow, although possibly not in the dimension considered in this study (e.g., Secor and Dean 1989; Francis and Campana 2004).

**The modified von Bertalanffy growth model with oblique linear asymptote**

Of the alternative somatic and otolith growth curves that were considered, the modified von Bertalanffy growth model with oblique linear asymptote provided the best representations of only the somatic growth of *B. frenchii* and the otolith growth of *G. hebraicum*, for both of which an initial rapid rate of growth was followed by a much reduced and more constant rate of growth. As noted above, the finding that somatic growth of *B. frenchii* was best represented by a modified von Bertalanffy growth curve is possibly explained by the small number of older fish within the observed age range of the sample to which the model was fitted, noting that the longevity of this species is 78 years\(^{19}\). Although it

\(^{19}\) Table S1
had been anticipated that the modified von Bertalanffy growth curve would provide the best representation of otolith radii at age for the different species, the flexible form of the Schnute (1981) model proved more capable of describing the data within the samples employed in this study.

**Distribution of lengths and otolith radii at age about growth curves**

It is typically assumed in studies of somatic growth of fish that deviations about the fitted length-at-age curve are additive and normally distributed with constant variance (Bowker 1995). In the case of *G. hebraicum*, however, Hesp et al. (2002) did fit a somatic growth curve that assumed increasing variance with age. This study has demonstrated, however, that, for some species, the assumption that deviations are additive and normally distributed with constant variance is invalid. Alternative statistical distributions, such as the lognormal, may provide a better description of sampled lengths at age, as found (by comparison of AICc scores) for *E. armatus* and *G. hebraicum*. While the statistical distributions that better described the variation around the otolith radius-at-age curves also varied among species, the lognormal distribution provided a better fit, i.e., lower AICc, than the normal distribution for five of the six species. This suggests that, for otolith growth, radii at age of most species are likely to exhibit increased variability around the fitted growth curves as age increases.

In this study, the relationship between fish length and otolith radius at age was that formed by the fish lengths and otolith radii predicted for fish of the same age using the somatic and otolith growth curves of the fitted bivariate model, rather than that formed empirically by observed lengths and ages at capture. This contrasts with the approach typically employed in more recent back-calculation studies where a relationship is fitted directly to lengths, otolith sizes and ages at capture for a sample of fish (Morita and
Matsuishi 2001; Finstad 2003; Vigliola and Meekan 2009). Such relationships appear to have been fitted without accounting for the ‘growth effect’, which Campana (1990) addressed by introducing the concept of a ‘biological intercept’. The improvement in fit provided by the inclusion in the bivariate growth model of such an intercept, as a constraint on the somatic and otolith growth curves, is the subject of a current investigation.

**Correlation between the deviations of fish lengths and otolith sizes at age from the two growth curves**

Although the maximum likelihood estimates of the correlations of the bivariate distributions were positive for all species and significantly greater than zero for *A. butcheri*, *E. coioides*, and *G. hebraicum*, this was not the case for *A. japonicus*, *B. frenchii* and *E. armatus*. It may be pertinent to this finding that, compared with the first three species, the lengths at age of individuals of *A. japonicus* and *B. frenchii* exhibited a far more rapid increase then more marked reduction in rate of increase relatively early within the ranges of their observed ages. For the last of these species, it may also be pertinent that deviations about the fitted somatic and otolith growth curves were considerably greater than for the other species.

The finding of a significant positive correlation between the deviations of the lengths and otolith radii of individuals of *A. butcheri*, *E. coioides*, and *G. hebraicum* from their predicted values parallels the results obtained for larval and juvenile stages of *Pomatomus saltatrix* by Hare and Cowen (1995), who, after allowing for age, demonstrated a positive correlation between deviations of fish size-on-age and otolith size-on-age. It should be noted, however, that the data considered in the current study comprised a wider age range that included both juveniles and adults of each species.
Relationships between expected total fish lengths and otolith sizes at age

The trend exhibited by the relationship between fish length and otolith radius reflects the rates at which the relative instantaneous rates of somatic and otolith growth decline with age. When the relative instantaneous rate of somatic growth lies below the corresponding rate of otolith growth, the rate of increase in fish length slows with increasing otolith radius, and the converse is true when the rate of somatic growth lies above that for otolith growth. If an inflection is apparent in the relationship between fish length and otolith radius (as with *G. hebraicum*), it results from the relative instantaneous rate of otolith growth declining from above the corresponding relative rate of somatic growth to below that rate, before then again increasing to above that rate.

Although the predicted relative instantaneous rates of somatic and otolith growth of all species declined with age towards zero, the growth curves that best described the lengths and otolith radii at age for a number of species were of forms that did not have finite asymptotes. It is suggested that, for those species, the paucity of older fish within the samples may have reduced the information available to determine reliably the form of the underlying relationship between size and age for older fish.

Numerous studies have recognized that the relationship between observed lengths of fish and the size of their otoliths is influenced by a ‘growth’ effect, which is associated with individual variation in somatic and otolith growth rates (e.g., Secor and Dean 1989; Reznick et al. 1989; Mugiya and Tanaka 1992). Thus, when fitting empirical relationships directly to lengths and otolith radii of fish at capture, as is typical in many back-calculation studies, an ‘errors in variables’ problem is encountered which, if not taken into account, introduces bias into the parameters of the fitted relationship (Xiao 1996). The ‘errors in variables’ problem is addressed by the bivariate growth model by fitting growth curves to length and otolith size at
age, and the correlation likely to exist between these errors is recognised by use of a bivariate statistical distribution of deviations from the respective growth curves. Through this approach, the bivariate growth model developed in the current study may produce a more reliable description of the relationship between fish length and otolith size than is produced by many of the approaches employed in earlier back-calculation studies.

Sclerochronological studies explore inter-annual variation in the ‘average’ widths of the annual growth increments in otoliths, after accounting for age effects and individual variation, and correlate the resulting otolith biochronologies with other time series of environmental or biological data (e.g., Guyette and Rabeni 1995; Black 2009; Ong et al. 2015). Such studies provide no direct information regarding inter-annual variation in somatic growth or its relationship with environmental variables, however, and thus, when drawing inferences regarding somatic growth, assume that otolith growth rate is an index of somatic growth rate and may be used as a proxy for that variable (e.g., Xiao 1996; Morrongiello et al. 2011; Black et al. 2013). There would be value, in future studies, in quantifying the extent to which the relationship between fish lengths and otolith sizes varies in response to different environmental variables, e.g., temperature. This might possibly be accomplished by extending the approach developed in this study by considering, within a mixed effects context, the inter-annual variation in growth parameters when fitting the somatic and otolith growth curves (e.g., Szalai et al. 2003; He and Bence 2007) and employing data from different systems or time periods and thereby taking the influence of environmental variables into account.

To summarise, this study has confirmed that the form of the relationship between expected fish length and otolith radius at age for juveniles and adults of a species is determined by the growth curves relating those two variables to age, and that the effect of age
should therefore be included when describing this relationship. A versatile growth curve, such as that of Schnute (1981) or chosen from a suite of alternative growth curves, and which allows for continued growth with age, should be employed when describing otolith size at age. The current study has demonstrated that, because of individual variation in both somatic and otolith growth rates, there is likely to be a positive correlation between the deviations of the lengths at age and otolith radii at age from their expected values. Because such correlation might exist, somatic and otolith growth curves should be fitted simultaneously assuming a bivariate distribution of the deviations from the growth curves and exploring alternative forms of marginal distributions, e.g., normal or lognormal.

**Acknowledgements**

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References


Hesp, S. A., Potter, I. C., and Hall, N. G. 2002. Age and size composition, growth rate, reproductive biology, and habitats of the West Australian dhufish (Glaucosoma hebraicum) and their relevance to the management of this species. Fish. Bull. 100(2): 214-227.


Table 1. Types of growth curves (and statistical distributions of errors) that, based on Akaike Information Criterion corrected for small sample size, best described total lengths and otolith radii at age of capture for *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides* and *Glaucosoma hebraicum*. $a$ and $b$ are parameters of the Schnute (1981) growth model. The modified von Bertalanffy curve has an oblique asymptote. AW = Akaike Weight.

<table>
<thead>
<tr>
<th>Species</th>
<th>Somatic growth</th>
<th>Otolith growth</th>
<th>Curve type</th>
<th>Error type</th>
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Table 2. Types of growth curves (and statistical distributions of errors) that, based on frequency of occurrence in bootstrap trials, best described total lengths and otolith radii at age of capture for Acanthopagrus butcheri, Argyrosomus japonicus, Bodianus frenchii, Epinephelides armatus, Epinephelus coioides and Glaucosoma hebraicum. Curve types are the same as described for Table 1. Bootstrap percentage = percentage of 4 000 trials for which the curve and error types were selected as best describing the bootstrap sample of lengths and ages at capture.

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<th>Species</th>
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Table 3. Values of parameters (\(a, b, y_1\) and \(y_2\)) and standard deviations (SD) for Schnute (1981) (normal font) and modified von Bertalanffy (oblique linear asymptote, bold font) somatic and otolith growth curves of the fitted bivariate models for *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides* and *Glaucosoma hebraicum*. SD = estimated standard deviation of marginal distribution of deviations from the respective growth curve. Curves were the same as those of Table 1. \(\tau_1\) = first reference age (youngest fish in the sample), \(\tau_2\) = second reference age (oldest fish in the sample), \(a\) and \(b\) = parameters of growth model, \(y_1\) = size at age \(\tau_1\), \(y_2\) = size at age \(\tau_2\). Standard errors (SE) of the parameters and of the standard deviations are presented in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Growth type</th>
<th>(a)</th>
<th>(b)</th>
<th>(y_1)</th>
<th>(y_2)</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acanthopagrus butcheri</em></td>
<td>Somatic</td>
<td>0.19</td>
<td>0.33</td>
<td>98</td>
<td>327</td>
<td>17</td>
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<tr>
<td>((\tau_1 = 0.62, \tau_2 = 19.62))</td>
<td></td>
<td>(SE = 0.02)</td>
<td>(SE = 6.69)</td>
<td>(SE = 7.25)</td>
<td>(SE = 1.67)</td>
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<tr>
<td>Otolith</td>
<td></td>
<td>0</td>
<td>2.03</td>
<td>0.41</td>
<td>1.65</td>
<td>0.06</td>
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<td></td>
<td></td>
<td>(SE = 0.16)</td>
<td>(SE = 0.01)</td>
<td>(SE = 0.04)</td>
<td>(SE = 0.01)</td>
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<tr>
<td><em>Argyrosomus japonicus</em></td>
<td>Somatic</td>
<td>0.24</td>
<td>1</td>
<td>154</td>
<td>1214</td>
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<td>((\tau_1 = 0.22, \tau_2 = 31.03))</td>
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<td>(SE = 0.02)</td>
<td>(SE = 39.37)</td>
<td>(SE = 27.21)</td>
<td>(SE = 7.92)</td>
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<tr>
<td>Otolith</td>
<td></td>
<td>0</td>
<td>1.64</td>
<td>0.57</td>
<td>10.21</td>
<td>0.09</td>
</tr>
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<td>(SE = 0.05)</td>
<td>(SE = 0.05)</td>
<td>(SE = 0.30)</td>
<td>(SE = 0.01)</td>
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<tr>
<td><em>Bodianus frenchii</em></td>
<td>Somatic</td>
<td>0.28</td>
<td>-0.38</td>
<td>90</td>
<td>420</td>
<td>21</td>
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<tr>
<td>((\tau_1 = 1.13, \tau_2 = 61.91))</td>
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<td>(SE = 0.05)</td>
<td>(SE = 0.53)</td>
<td>(SE = 15.42)</td>
<td>(SE = 12.55)</td>
<td>(SE = 2.07)</td>
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<tr>
<td>Otolith</td>
<td>0</td>
<td>1.78 (SE = 0.16)</td>
<td>0.36 (SE = 0.02)</td>
<td>2.09 (SE = 0.08)</td>
<td>0.09 (SE = 0.01)</td>
<td></td>
</tr>
<tr>
<td>-----------</td>
<td>----------</td>
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<td>------------------</td>
<td>------------------</td>
<td>------------------</td>
<td></td>
</tr>
<tr>
<td><em>Epinephelides armatus</em></td>
<td>Somatic</td>
<td>0.38 (SE = 0.05)</td>
<td>-1 (SE = 0.05)</td>
<td>149 (SE = 9.75)</td>
<td>482 (SE = 21.85)</td>
<td>0.11 (SE = 0.01)</td>
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<tr>
<td></td>
<td>Otolith</td>
<td>0.33 (SE = 0.08)</td>
<td>1 (SE = 0.04)</td>
<td>0.52 (SE = 0.04)</td>
<td>1.06 (SE = 0.04)</td>
<td>0.10 (SE = 0.01)</td>
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<tr>
<td><em>Epinephelus coioides</em></td>
<td>Somatic</td>
<td>0.12 (SE = 0.02)</td>
<td>1 (SE = 0.03)</td>
<td>70 (SE = 19.55)</td>
<td>1059 (SE = 29.36)</td>
<td>61 (SE = 6.13)</td>
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<td></td>
<td>Otolith</td>
<td>0.15 (SE = 0.02)</td>
<td>1 (SE = 0.03)</td>
<td>0.35 (SE = 0.05)</td>
<td>1.87 (SE = 0.05)</td>
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<tr>
<td><em>Glaucosoma hebraicum</em></td>
<td>Somatic</td>
<td>0 (SE = 0.19)</td>
<td>1.90 (SE = 0.19)</td>
<td>105 (SE = 7.79)</td>
<td>992 (SE = 43.73)</td>
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<td></td>
<td>Otolith</td>
<td>1.31 (SE = 0.38)</td>
<td>0.22 (SE = 0.16)</td>
<td>0.74 (SE = 0.04)</td>
<td>3.42 (SE = 0.12)</td>
<td>0.09 (SE = 0.01)</td>
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</table>
**Table 4.** Negative log-likelihood (NLL) for the fitted bivariate growth models for *Acanthopagrus butcheri, Argyrosomus japonicus, Bodianus frenchii, Epinephelides armatus, Epinephelus coioides* and *Glaucosoma hebraicum*, together with correlation $\rho$ of the bivariate distribution of deviations from the somatic and otolith growth curves. Standard errors (SE) of the correlation are presented in parentheses. ‘$P\{\rho > 0\}$’ = P-value of one-tailed t-test that $\rho > 0$. ‘Prop. of bootstraps $> 0$’ = proportion of 4 000 bootstrap trials for which the point estimate of the correlation coefficient exceeded zero.

<table>
<thead>
<tr>
<th>Species</th>
<th>NLL</th>
<th>$\rho$</th>
<th>$P{\rho &gt; 0}$</th>
<th>Prop. of bootstraps $&gt; 0$</th>
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<td><em>Acanthopagrus butcheri</em></td>
<td>141</td>
<td>0.31</td>
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<td>0.97</td>
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<td><em>Argyrosomus japonicus</em></td>
<td>299</td>
<td>0.13</td>
<td>0.43</td>
<td>0.89</td>
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<td></td>
<td></td>
<td>(SE = 0.14)</td>
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<tr>
<td><em>Bodianus frenchii</em></td>
<td>169</td>
<td>0.06</td>
<td>0.73</td>
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<tr>
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<td>(SE = 0.14)</td>
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<td><em>Epinephelides armatus</em></td>
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<td>0.22</td>
<td>0.15</td>
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<td></td>
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</tr>
<tr>
<td><em>Epinephelus coioides</em></td>
<td>228</td>
<td>0.50</td>
<td>0.00</td>
<td>1</td>
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<tr>
<td></td>
<td></td>
<td>(SE = 0.11)</td>
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<td></td>
</tr>
<tr>
<td><em>Glaucosoma hebraicum</em></td>
<td>253</td>
<td>0.63</td>
<td>0.00</td>
<td>1</td>
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<td>(SE = 0.09)</td>
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</table>
Figure captions

Figure 1. Growth curves fitted to the total lengths (mm) at ages of capture (years) for *Acanthopagrus butcheri, Argyrosomus japonicus, Bodianus frenchii, Epinephelides armatus, Epinephelus coioides* and *Glaucosoma hebraicum*.

Figure 2. Growth curves fitted to the otolith radii (mm) at ages of capture (years) for *Acanthopagrus butcheri, Argyrosomus japonicus, Bodianus frenchii, Epinephelides armatus, Epinephelus coioides* and *Glaucosoma hebraicum*.

Figure 3. Total lengths (mm) and otolith radii (mm) at capture for *Acanthopagrus butcheri, Argyrosomus japonicus, Bodianus frenchii, Epinephelides armatus, Epinephelus coioides* and *Glaucosoma hebraicum*, and the relationships formed by the pairs of values of total length and otolith radius at each age (over the range of observed ages at capture) predicted for each species using the somatic and otolith growth curves of the fitted bivariate growth model for that species.

Figure 4. Relative instantaneous rates of somatic and otolith growth versus age (years) at capture for *Acanthopagrus butcheri, Argyrosomus japonicus, Bodianus frenchii, Epinephelides armatus, Epinephelus coioides* and *Glaucosoma hebraicum*. Solid line (−) represents somatic growth and dashed line (---) represents otolith growth.
Figure 1. Growth curves fitted to the total lengths (mm) at ages of capture (years) for Acanthopagrus butcheri, Argyrosomus japonicus, Bodianus frenchii, Epinephelides armatus, Epinephelus coioides and Glaucosoma hebraicum.

279x361mm (300 x 300 DPI)
Figure 2. Growth curves fitted to the otolith radii (mm) at ages of capture (years) for Acanthopagrus butcheri, Argyrosomus japonicus, Bodianus frenchii, Epinephelides armatus, Epinephelus coioides and Glaucosoma hebraicum.

279x361mm (300 x 300 DPI)
Figure 3. Total lengths (mm) and otolith radii (mm) at capture for Acanthopagrus butcheri, Argyrosomus japonicus, Bodianus frenchii, Epinephelides armatus, Epinephelus coioides and Glaucosoma hebraicum, and the relationships formed by the pairs of values of total length and otolith radius at each age (over the range of observed ages at capture) predicted for each species using the somatic and otolith growth curves of the fitted bivariate growth model for that species.
Figure 4. Relative instantaneous rates of somatic and otolith growth versus age (years) at capture for Acanthopagrus butcheri, Argyrosomus japonicus, Bodianus frenchii, Epinephelides armatus, Epinephelus coioides and Glaucosoma hebraicum. Solid line (-) represents somatic growth and dashed line (---) represents otolith growth.
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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.

<table>
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<tr>
<th>Species</th>
<th>Max. age (years)</th>
<th>Max. TL (mm)</th>
<th>Sexuality</th>
<th>Habitat</th>
<th>References</th>
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<tr>
<td>Acanthopagrus butcheri</td>
<td>31</td>
<td>530</td>
<td>Gonochorist</td>
<td>Temperate estuaries</td>
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<td></td>
<td>Jenkins et al. (2006)</td>
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<td>Potter et al. (2008)</td>
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<td>Argyrosomus japonicus</td>
<td>31</td>
<td>2000</td>
<td>Gonochorist</td>
<td>Coastal marine waters, seasonally entering estuaries</td>
<td>Farmer et al. (2005)</td>
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<td></td>
<td></td>
<td></td>
<td>Gomon et al. (2008)</td>
</tr>
<tr>
<td>Bodianus frenchii</td>
<td>78</td>
<td>480</td>
<td>Protogynous hermaphrodite</td>
<td>Over and around coastal temperate reefs</td>
<td>Gomon et al. (2008)</td>
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<td></td>
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<td></td>
<td>Cossington et al. (2010)</td>
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<td></td>
<td>Platell et al. (2010)</td>
</tr>
<tr>
<td>Epinephelides armatus</td>
<td>19</td>
<td>510</td>
<td>Gonochorist</td>
<td>Over and around coastal temperate reefs</td>
<td>Moore et al. (2007)</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Gomon et al. (2008)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Platell et al. (2010)</td>
</tr>
<tr>
<td>Epinephelus coioides</td>
<td>22</td>
<td>1110</td>
<td>Protogynous hermaphrodite</td>
<td>Subtropical/tropical mangrove nursery habitats and coastal reefs</td>
<td>Heemstra and Randall (1993)</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>Heemstra (1995)</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td>Pember et al. (2005)</td>
</tr>
<tr>
<td>Glaucosoma hebraicum</td>
<td>41</td>
<td>1120</td>
<td>Gonochorist</td>
<td>Temperate coastal marine waters, around reefs</td>
<td>Hesp et al. (2002)</td>
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<td>Lenanton et al. (2009)</td>
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<td></td>
<td>Platell et al. (2010)</td>
</tr>
</tbody>
</table>
References for Table S1


https://mc06.manuscriptcentral.com/cjfas-pubs


Supplemental material S1. Sampling regime used for the collection of *Acanthopagrus butcheri*.

*Acanthopagrus butcheri* was sampled in the Wellstead Estuary at 34°50’S latitude and 118°60’E longitude on the south coast of Western Australia in May 2013 using seine and gill nets. The seine net was 21.5 m long and comprised two 10 m long wings (6 m of 9 mm mesh and 4 m of 3 mm mesh) and a 1.5 m wide bunt of 3 mm mesh. This net, which was deployed during daylight, fished to a depth of ~ 1.5 m and swept an area of ~ 116 m². The sunken composite multifilament gill net comprised seven 20 m long panels, each with a height of 2 m and containing a different stretched mesh size, i.e., 51, 63, 76, 89, 102, 115 or 127 mm mesh. Gill nets were set parallel to the shore at dusk and retrieved ~ 2 to 3 h later. Fish were euthanized in an ice slurry immediately after capture and transported to the laboratory where they were frozen until processed.
**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.

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

**References for Table S2**


Hesp, S. A., Potter, I. C., and Hall, N. G. 2002. Age and size composition, growth rate, reproductive biology, and habitats of the West Australian dhufish (Glaucosoma hebraicum) and their relevance to the management of this species. Fish. Bull. 100(2): 214-227.


Table S3. Birth dates assigned to each of *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides* and *Glaucosoma hebraicum* in estuarine and coastal waters along the coast of Western Australia.

<table>
<thead>
<tr>
<th>Species</th>
<th>Date of birth</th>
<th>References</th>
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</thead>
<tbody>
<tr>
<td><em>Acanthopagrus butcheri</em></td>
<td>1 October</td>
<td>Sarre and Potter (2000)</td>
</tr>
<tr>
<td><em>Argyrosomus japonicus</em></td>
<td>1 July on upper west coast</td>
<td>Farmer (2008)</td>
</tr>
<tr>
<td></td>
<td>1 December on lower west coast</td>
<td></td>
</tr>
<tr>
<td><em>Bodianus frenchii</em></td>
<td>1 January</td>
<td>Cossington et al. (2010)</td>
</tr>
<tr>
<td><em>Epinephelides armatus</em></td>
<td>1 February</td>
<td>Moore et al. (2007)</td>
</tr>
<tr>
<td><em>Epinephelus coioides</em></td>
<td>1 January</td>
<td>Pember et al. (2005)</td>
</tr>
<tr>
<td><em>Glaucosoma hebraicum</em></td>
<td>1 February</td>
<td>Hesp et al. (2002)</td>
</tr>
</tbody>
</table>

References for Table S3


Supplemental material S2. Special cases of the Schnute (1981) growth equation that are equivalent to common growth curves.

Curves of a range of different forms, encapsulated within the Schnute model and fitted to the lengths and otolith radii at ages of capture, were compared to determine the growth curve which provided the best description for each of these variables. The growth curves tested included the following:

The generalised von Bertalanffy growth curve, obtained by setting values of $a > 0$ and $b > 0$ in the Schnute model, may be written as

$$Y(t) = y_\infty (1 - \exp[-g(t - t_0)])^p$$

where, in this equation and the equations that follow, $Y(t)$ represents size at age $t$, and $y_\infty$, $g$, $p$ and $t_0$ are parameters with $y_\infty > 0$, $g > 0$ and $p > 0$ (Schnute 1981). When $p = 1$, i.e., when $a > 0$, $b = 1$, the above equation becomes the traditional von Bertalanffy curve used to describe the growth of fish. When $p = 3$, the curve is the Pütter number 2 growth curve, which is often used to describe growth of fish in terms of mass.

The Richards growth curve, obtained using values of $a > 0$ and $b < 0$, is

$$Y(t) = y_\infty \left(1 - \frac{1}{p} \exp[-g(t - t_0)]\right)^{-p}$$

The Gompertz growth curve, obtained using values of $a > 0$ and $b = 0$, is

$$Y(t) = y_\infty \exp(-\exp[-g(t - t_0)])$$

The logistic growth curve, obtained using values of $a > 0$ and $b = -1$, is

$$Y(t) = y_\infty \left(1 + \exp[-g(t - t_0)]\right)^{-1}$$
The linear growth curve, obtained using values of $a = 0$ and $b = 1$, is

$$Y(t) = g(t - t_0)$$  \hspace{1cm} (5)

The quadratic growth curve, obtained using values of $a = 0$ and $b = \frac{1}{2}$, with $\beta > 0$, is

$$Y(t) = (\alpha + \beta t)^2$$  \hspace{1cm} (6)

The $t^{th}$ power growth curve, obtained using values of $a = 0$ and $b = 0$, with $\alpha > 0$ and $\beta > 0$, is

$$Y(t) = \alpha \beta^t$$  \hspace{1cm} (7)

The exponential growth curve, obtained using values of $a < 0$ and $b = 1$, with $\beta > 0$ and $\gamma > 0$, is

$$Y(t) = \alpha + \beta \exp(\gamma t)$$  \hspace{1cm} (8)

Reference for Supplemental material S2

Table S4. The parameter space \((a, b)\) for the Schnute (1981) growth curve was divided into nine regions such that, when fitting the model, parameters estimates could be constrained to each region. This avoided any discontinuity in derivatives that would have resulted if tests to determine whether to employ an equation with an alternative structure had been included in the Template Model Builder (TMB) code.

<table>
<thead>
<tr>
<th>Region</th>
<th>Parameter space</th>
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<td>1</td>
<td>(a &gt; 0) and (b &gt; 0)</td>
</tr>
<tr>
<td>2</td>
<td>(a &gt; 0) and (b &lt; 0)</td>
</tr>
<tr>
<td>3</td>
<td>(a &lt; 0) and (b &gt; 0)</td>
</tr>
<tr>
<td>4</td>
<td>(a &lt; 0) and (b &lt; 0)</td>
</tr>
<tr>
<td>5</td>
<td>(a &gt; 0) and (b = 0)</td>
</tr>
<tr>
<td>6</td>
<td>(a &lt; 0) and (b = 0)</td>
</tr>
<tr>
<td>7</td>
<td>(a = 0) and (b &gt; 0)</td>
</tr>
<tr>
<td>8</td>
<td>(a = 0) and (b &lt; 0)</td>
</tr>
<tr>
<td>9</td>
<td>(a = 0) and (b = 0)</td>
</tr>
</tbody>
</table>

Note. Several regions described in this table, and defined by the constraints imposed on the parameters \(a\) and \(b\), were the same as those of the specific common growth curves described by Schnute (1981), i.e., the Region 1 curve (above) is equivalent to the generalized von Bertalanffy curve, the Region 2 curve is equivalent to the Richards growth curve, the Region 5 curve is equivalent to the Gompertz growth curve and the Region 9 curve is equivalent to the \(t^{th}\) power curve\(^1\).

\(^1\) Supplemental material S2
Reference for Table S4

Supplemental material S3. Univariate and bivariate probability density functions

Univariate normal distribution

If $y$ is normally-distributed with mean $\mu$ and standard deviation $\sigma$, i.e., $y \sim N(\mu, \sigma^2)$, the probability density function may be written as

$$pdf(y|\mu, \sigma) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(y - \mu)^2}{2\sigma^2}\right].$$

The negative log-likelihood of observed values $y_j$, where $j = 1, 2, ..., n$, may be calculated as

$$\lambda = (n/2)[\ln(2\pi) + \ln(\sigma^2)] + \frac{1}{2\sigma^2} \sum_{j=1}^{n} (y_j - \mu)^2.$$

Univariate lognormal distribution

If $y$ has a lognormal distribution with mean $\mu$ and standard deviation $\sigma$, i.e., $y \sim LN(\mu, \sigma^2)$, the probability density function (Burnham and Anderson 2002) may be written as

$$pdf(y|\mu, \sigma) = \frac{1}{y\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(\ln(y) - \mu)^2}{2\sigma^2}\right].$$

The negative log-likelihood of observed values $y_j$, where $j = 1, 2, ..., n$, may be calculated as

$$\lambda = (n/2)[\ln(2\pi) + \ln(\sigma^2)] + \frac{1}{2\sigma^2} \sum_{j=1}^{n} (y_j - \mu)^2 + \sum_{j=1}^{n} \ln(y_j).$$

Bivariate normal distribution

If $y_1$ and $y_2$ have a bivariate normal distribution with means of $\mu_1$ and $\mu_2$, respectively, and standard deviations $\sigma_1$ and $\sigma_2$, respectively, and with correlation coefficient...
\[ \rho, \text{i.e., } (y_1, y_2) \sim \text{BVN}(\mu_1, \mu_2, \sigma_1^2, \sigma_2^2, \rho), \text{ then the probability density function of the joint distribution of these two variables is} \]

\[
pdf(y_1, y_2 | \mu_1, \mu_2, \sigma_1, \sigma_2, \rho) = \frac{1}{2\pi \sqrt{(1 - \rho^2)\sigma_1^2 \sigma_2^2}} \exp \left[ -\frac{z}{2(1 - \rho^2)} \right]
\]

where

\[ z = (A^2 - 2\rho AB + B^2), \]

\[ A = \frac{y_1 - \mu_1}{\sigma_1} \]

and

\[ B = \frac{y_2 - \mu_2}{\sigma_2} \]

The negative log-likelihood of observed pairs of values \( y_{1j} \) and \( y_{2j} \), where \( j = 1, 2, \ldots, n \), may be calculated as

\[ \lambda = n \ln \left(2\pi \sigma_1 \sigma_2 \sqrt{1 - \rho^2} \right) + \frac{1}{2(1 - \rho^2)} \sum_{j=1}^{n} \left[ \frac{\sigma_1^2}{\sigma_2} (y_{2j} - \mu_2) \right]. \]

The conditional distribution of \( y_1 \) given \( y_2 \) is the normal distribution with:

- Mean: \( \mu_1 + \rho \frac{\sigma_1}{\sigma_2} (y_2 - \mu_2) \)
- Variance: \( \sigma_1^2 (1 - \rho^2) \)

**Bivariate lognormal distribution**

If \( y_1 \) and \( y_2 \) have a bivariate lognormal distribution (e.g., Cheng 1986) with means of \( \mu_1 \) and \( \mu_2 \), respectively, and standard deviations \( \sigma_1 \) and \( \sigma_2 \), respectively, and with correlation coefficient \( \rho \), i.e., \( (y_1, y_2) \sim \text{BVLN}(\mu_1, \mu_2, \sigma_1^2, \sigma_2^2, \rho) \), then the probability density function of the joint distribution of these two variables is
\[
\text{pdf}(y_1, y_2 | \mu_1, \mu_2, \sigma_1, \sigma_2, \rho) = \frac{1}{2\pi y_1 y_2 \sqrt{(1 - \rho^2)\sigma_1^2 \sigma_2^2}} \exp \left[ -\frac{z}{2(1 - \rho^2)} \right]
\]

where

\[
z = (A^2 - 2\rho AB + B^2),
\]

\[
A = \frac{\ln(y_1) - \mu_1}{\sigma_1}
\]

and

\[
B = \frac{\ln(y_2) - \mu_2}{\sigma_2}.
\]

The negative log-likelihood of observed pairs of values \(y_{1j}\) and \(y_{2j}\), where \(j = 1, 2, ..., n\), may be calculated as

\[
\lambda = n \ln \left( 2\pi \sigma_1 \sigma_2 \sqrt{1 - \rho^2} \right) + \frac{1}{2(1 - \rho^2)} \sum_{j=1}^{n} z_j + \sum_{j=1}^{n} \ln(y_{1j}) + \sum_{j=1}^{n} \ln(y_{2j}).
\]

The conditional distribution of \(y_1\), given \(y_2\), is the lognormal distribution

\[
y_1 \sim \text{LN} \left( \mu_1 + \rho \frac{\sigma_1}{\sigma_2} (\ln(y_2) - \mu_2), \sigma_1^2 (1 - \rho^2) \right),
\]

where the probability density function of this distribution is

\[
\text{pdf}(y_1 | y_2, \mu_1, \mu_2, \sigma_1, \sigma_2, \rho)
\]

\[
= \frac{1}{\sqrt{2\pi(1 - \rho^2)\sigma_1} y_1} \exp \left[ -\frac{1}{2} \left( \ln(y_1) - \left[ \mu_1 + \rho \frac{\sigma_1}{\sigma_2} (\ln(y_2) - \mu_2) \right] \right)^2 \sigma_1^2 (1 - \rho^2) \right].
\]
Bivariate normal-lognormal distribution

If \( y_1 \) and \( y_2 \) have a bivariate normal-lognormal distribution, where \( y_1 \) is normally distributed with mean of \( \mu_1 \) and standard deviations \( \sigma_1 \) and \( y_2 \) has a lognormal distribution with mean of \( \mu_2 \) and standard deviations \( \sigma_2 \), and with correlation coefficient between \( y_1 \) and \( \ln(y_2) \) of \( \rho \), i.e., \((y_1, y_2) \sim \text{N}LN(\mu_1, \mu_2, \sigma_1^2, \sigma_2^2, \rho)\), then, as advised by Chen and Holtby (2002), the probability density function of the joint distribution of these two variables is

\[
\text{pdf}(y_1, y_2 | \mu_1, \mu_2, \sigma_1, \sigma_2, \rho) = \frac{1}{2\pi y_2 \sqrt{(1-\rho^2)\sigma_1^2 \sigma_2^2}} \exp\left[-\frac{z}{2(1-\rho^2)}\right]
\]

where

\[
z = (A^2 - 2\rho AB + B^2),
A = \frac{y_1 - \mu_1}{\sigma_1},
B = \frac{\ln(y_2) - \mu_2}{\sigma_2}.
\]

The negative log-likelihood of observed pairs of values \( y_{1j} \) and \( y_{2j} \), where \( j = 1, 2, ..., n \), may be calculated as

\[
\lambda = n \ln\left(2\pi \sigma_1 \sigma_2 \sqrt{1-\rho^2}\right) + \frac{1}{2(1-\rho^2)} \sum_{j=1}^{n} \ln(z_j) + \sum_{j=1}^{n} \ln(y_{2j}).
\]

Note that the negative log-likelihood of the bivariate lognormal-normal distribution may be obtained from the above equations for the bivariate normal-lognormal distribution by reversing the order of the two variables.
The conditional distribution of $y_1$, given $y_2$, is the normal distribution with:

$$\text{Mean: } \mu_1 + \rho \frac{\sigma_1}{\sigma_2} (\ln(y_2) - \mu_2). \quad \text{Variance: } \sigma_1^2 (1 - \rho^2).$$

The conditional distribution of $y_2$, given $y_1$, is the lognormal distribution

$$y_2 \sim \text{LN}\left( \mu_2 + \rho \frac{\sigma_2}{\sigma_1} (y_1 - \mu_1), \sigma_2^2 (1 - \rho^2) \right),$$

where the probability density function of this lognormal distribution is:

$$\text{pdf}(y_2|y_1, \mu_1, \mu_2, \sigma_1, \sigma_2, \rho) = \frac{1}{\sqrt{2\pi (1 - \rho^2)} \sigma_2 y_2} \exp \left[ -\frac{1}{2} \left( \frac{\ln(y_2) - \left[ \mu_2 + \rho \frac{\sigma_2}{\sigma_1} (y_1 - \mu_1) \right]}{\sigma_2^2 (1 - \rho^2)} \right)^2 \right].$$

Reference for Supplemental material S3


Table S5. Values of corrected Akaike Information Criteria (AICc) and Akaike Weights (AWs) for somatic growth curves of different functional forms (i.e., a modified version of the von Bertalanffy growth equation and, for all other curve types, the versatile growth model described by Schnute (1981)) fitted to total lengths (mm) at ages of capture for 50 individuals of *Acanthopagrus butcheri* collected from Wellstead Estuary in 2013, where the models assumed a normal distribution or lognormal distribution of deviations from expected lengths at age.

<table>
<thead>
<tr>
<th>Curve type</th>
<th>Normal distribution</th>
<th>Lognormal distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AICc</td>
<td>AW</td>
</tr>
<tr>
<td>Modified von Bertalanffy</td>
<td>434.70</td>
<td>0.01</td>
</tr>
<tr>
<td>Generalised von Bertalanffy</td>
<td>434.57</td>
<td>0.07</td>
</tr>
<tr>
<td>Traditional von Bertalanffy</td>
<td>432.22</td>
<td>0.23</td>
</tr>
<tr>
<td>Püttler number 2</td>
<td><strong>432.19</strong></td>
<td><strong>0.24</strong></td>
</tr>
<tr>
<td>Gompertz</td>
<td>432.46</td>
<td>0.21</td>
</tr>
<tr>
<td>Richards</td>
<td>434.94</td>
<td>0.06</td>
</tr>
<tr>
<td>Logistic</td>
<td>433.92</td>
<td>0.10</td>
</tr>
<tr>
<td>Linear</td>
<td>489.04</td>
<td>0.00</td>
</tr>
<tr>
<td>Quadratic</td>
<td>500.87</td>
<td>0.00</td>
</tr>
<tr>
<td>t&lt;sup&gt;th&lt;/sup&gt; power</td>
<td>509.73</td>
<td>0.00</td>
</tr>
<tr>
<td>Exponential</td>
<td>491.46</td>
<td>0.00</td>
</tr>
<tr>
<td>a &lt; 0 and b &gt; 0</td>
<td>441.08</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>a &lt; 0 and b &lt; 0</td>
<td>514.61</td>
<td>0.00</td>
</tr>
<tr>
<td>a &lt; 0 and b = 0</td>
<td>512.13</td>
<td>0.00</td>
</tr>
<tr>
<td>a = 0 and b &gt; 0</td>
<td>438.60</td>
<td>0.01</td>
</tr>
<tr>
<td>a = 0 and b &lt; 0</td>
<td>512.10</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Note. Bold font is used to identify the growth curve with the lowest AICc.
Reference for Table S5

Table S6. Quantitatively similar somatic growth curves, i.e., curves with values of corrected Akaike Information Criteria (AICc) lying within 2 units of the AICc (in bold font) of the best-fitting (i.e., lowest AICc) curve, for each of *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides* and *Glaucosoma hebraicum*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Curve type</th>
<th>Distribution type</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acanthopagrus butcheri</em></td>
<td>Pütter number 2</td>
<td>normal</td>
<td>432.19</td>
</tr>
<tr>
<td></td>
<td>Traditional von Bertalanffy</td>
<td>normal</td>
<td>432.22</td>
</tr>
<tr>
<td></td>
<td>Gompertz</td>
<td>normal</td>
<td>432.46</td>
</tr>
<tr>
<td></td>
<td>Logistic</td>
<td>normal</td>
<td>433.92</td>
</tr>
<tr>
<td><em>Argyrosomus japonicus</em></td>
<td>Traditional von Bertalanffy</td>
<td>normal</td>
<td>587.93</td>
</tr>
<tr>
<td></td>
<td>Pütter number 2</td>
<td>normal</td>
<td>589.12</td>
</tr>
<tr>
<td><em>Bodianus frenchii</em></td>
<td>Modified von Bertalanffy</td>
<td>normal</td>
<td>456.11</td>
</tr>
<tr>
<td></td>
<td>Modified von Bertalanffy</td>
<td>lognormal</td>
<td>456.25</td>
</tr>
<tr>
<td><em>Epinephelides armatus</em></td>
<td>Logistic</td>
<td>lognormal</td>
<td>508.08</td>
</tr>
<tr>
<td><em>Epinephelus coioides</em></td>
<td>Traditional von Bertalanffy</td>
<td>normal</td>
<td>562.38</td>
</tr>
<tr>
<td></td>
<td>Pütter number 2</td>
<td>normal</td>
<td>564.37</td>
</tr>
<tr>
<td><em>Glaucosoma hebraicum</em></td>
<td>$a = 0$ and $b &gt; 0$</td>
<td>lognormal</td>
<td>564.78</td>
</tr>
</tbody>
</table>
Table S7. Values of corrected Akaike Information Criteria (AICc) and Akaike Weights (AWs) for otolith growth curves of different functional forms (i.e., a modified version of the von Bertalanffy growth equation and, for all other curve types, the versatile growth model described by Schnute (1981)) fitted to otolith radii (mm) at ages of capture for 50 individuals of *Acanthopagrus butcheri* collected from Wellstead Estuary in 2013, where the models assumed a normal distribution or lognormal distribution of deviations from expected radii at age.

<table>
<thead>
<tr>
<th>Curve type</th>
<th>Normal distribution</th>
<th>Lognormal distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Modified von Bertalanffy</td>
<td>-115.79</td>
<td>-123.51</td>
</tr>
<tr>
<td>Generalised von Bertalanffy</td>
<td>-115.94</td>
<td>-124.48</td>
</tr>
<tr>
<td>Traditional von Bertalanffy</td>
<td>-118.26</td>
<td>-123.87</td>
</tr>
<tr>
<td>Pütter number 2</td>
<td>-117.34</td>
<td>-120.02</td>
</tr>
<tr>
<td>Gompertz</td>
<td>-116.62</td>
<td>-117.84</td>
</tr>
<tr>
<td>Richards</td>
<td>-114.15</td>
<td>-115.37</td>
</tr>
<tr>
<td>Logistic</td>
<td>-113.80</td>
<td>-111.33</td>
</tr>
<tr>
<td>Linear</td>
<td>-87.04</td>
<td>-88.83</td>
</tr>
<tr>
<td>Quadratic</td>
<td>-67.23</td>
<td>-57.83</td>
</tr>
<tr>
<td>t&lt;sup&gt;a&lt;/sup&gt; power</td>
<td>-52.15</td>
<td>-32.88</td>
</tr>
<tr>
<td>Exponential</td>
<td>-84.60</td>
<td>-86.39</td>
</tr>
<tr>
<td>a &lt; 0 and b &gt; 0</td>
<td>-115.45</td>
<td>-124.56</td>
</tr>
<tr>
<td>a &lt; 0 and b &lt; 0</td>
<td>-47.25</td>
<td>47.22</td>
</tr>
<tr>
<td>a &lt; 0 and b = 0</td>
<td>-49.73</td>
<td>-30.46</td>
</tr>
<tr>
<td>a = 0 and b &gt; 0</td>
<td>-117.93</td>
<td><strong>-126.95</strong></td>
</tr>
<tr>
<td>a = 0 and b &lt; 0</td>
<td>-49.78</td>
<td>-30.51</td>
</tr>
</tbody>
</table>

Note. Bold font is used to identify the growth curve with the lowest AICc.
Reference for Table S7

**Table S8.** Quantitatively similar otolith growth curves, i.e., curves with values of corrected Akaike Information Criteria (AICc) lying within 2 units of the AICc (in bold font) of the best-fitting (i.e., lowest AICc) curve, for each of *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides* and *Glaucosoma hebraicum*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Curve type</th>
<th>Distribution type</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acanthopagrus butcheri</em></td>
<td>$a = 0$ and $b &gt; 0$</td>
<td>lognormal</td>
<td>-126.95</td>
</tr>
<tr>
<td><em>Argyrosomus japonicus</em></td>
<td>$a = 0$ and $b &gt; 0$</td>
<td>lognormal</td>
<td>29.49</td>
</tr>
<tr>
<td><em>Bodianus frenchii</em></td>
<td>$a = 0$ and $b &gt; 0$</td>
<td>lognormal</td>
<td>-97.07</td>
</tr>
<tr>
<td></td>
<td>Modified von Bertalanffy</td>
<td>lognormal</td>
<td>-95.82</td>
</tr>
<tr>
<td></td>
<td>$a &lt; 0$ and $b &gt; 0$</td>
<td>lognormal</td>
<td>-96.35</td>
</tr>
<tr>
<td><em>Epinephelides armatus</em></td>
<td>Traditional von Bertalanffy</td>
<td>lognormal</td>
<td>-91.97</td>
</tr>
<tr>
<td></td>
<td>Pütter number 2</td>
<td>lognormal</td>
<td>-91.77</td>
</tr>
<tr>
<td></td>
<td>Gompertz</td>
<td>lognormal</td>
<td>-91.64</td>
</tr>
<tr>
<td></td>
<td>$a = 0$ and $b &gt; 0$</td>
<td>lognormal</td>
<td>-91.24</td>
</tr>
<tr>
<td></td>
<td>Logistic</td>
<td>lognormal</td>
<td>-91.21</td>
</tr>
<tr>
<td></td>
<td>Modified von Bertalanffy</td>
<td>lognormal</td>
<td>-90.63</td>
</tr>
<tr>
<td><em>Epinephelus coioides</em></td>
<td>Traditional von Bertalanffy</td>
<td>normal</td>
<td>-74.41</td>
</tr>
<tr>
<td></td>
<td>$a = 0$ and $b &gt; 0$</td>
<td>normal</td>
<td>-74.31</td>
</tr>
<tr>
<td></td>
<td>Modified von Bertalanffy</td>
<td>normal</td>
<td>-74.20</td>
</tr>
<tr>
<td></td>
<td>Generalised von Bertalanffy</td>
<td>normal</td>
<td>-73.77</td>
</tr>
<tr>
<td><em>Glaucosoma hebraicum</em></td>
<td>Modified von Bertalanffy</td>
<td>lognormal</td>
<td>-13.15</td>
</tr>
<tr>
<td></td>
<td>$a &lt; 0$ and $b &gt; 0$</td>
<td>lognormal</td>
<td>-11.36</td>
</tr>
</tbody>
</table>
Table S9. Values of adjusted coefficients of determination ($R^2_{\text{adjusted}}$) for the curves for total lengths and otolith radii at age of the fitted bivariate growth model for each of *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides* and *Glaucosoma hebraicum*, where the somatic and otolith growth curves were of the forms (and possessing the statistical distribution for deviations) that produced the lowest values of AICc.

<table>
<thead>
<tr>
<th>Species</th>
<th>$R^2_{\text{adjusted}}$</th>
<th>Total length</th>
<th>Otolith radius</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acanthopagrus butcheri</em></td>
<td>0.92</td>
<td>0.94</td>
<td></td>
</tr>
<tr>
<td><em>Argyrosomus japonicus</em></td>
<td>0.92</td>
<td>0.96</td>
<td></td>
</tr>
<tr>
<td><em>Bodianus frenchii</em></td>
<td>0.91</td>
<td>0.94</td>
<td></td>
</tr>
<tr>
<td><em>Epinephelides armatus</em></td>
<td>0.79</td>
<td>0.53</td>
<td></td>
</tr>
<tr>
<td><em>Argyrosomus japonicus</em></td>
<td>0.95</td>
<td>0.94</td>
<td></td>
</tr>
<tr>
<td><em>Glaucosoma hebraicum</em></td>
<td>0.88</td>
<td>0.87</td>
<td></td>
</tr>
</tbody>
</table>
Table S10. Ranges of negative log-likelihoods (NLL) for the bivariate growth models produced using the quantitatively similar somatic and otolith growth curves for *Acanthopagrus butcheri, Argyrosomus japonicus, Bodianus frenchii, Epinephelides armatus, Epinephelus coioides* and *Glaucosoma hebraicum*, together with ranges of both the correlations ($\rho$) between deviations from the growth curves for those bivariate models and the P-values, $P(\rho > 0)$, of one-tailed t-tests that those correlations exceed zero. Quantitatively similar curves were those with AICc scores lying within 2 units of the lowest score, i.e., the AICc of the fitted curve that best described the data.

<table>
<thead>
<tr>
<th>Species</th>
<th>NLL</th>
<th>$\rho$</th>
<th>$P(\rho &gt; 0)$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acanthopagrus butcheri</em></td>
<td>141-142</td>
<td>0.31-0.31</td>
<td>0.04-0.05</td>
</tr>
<tr>
<td><em>Argyrosomus japonicus</em></td>
<td>299-300</td>
<td>0.12-0.13</td>
<td>0.42-0.45</td>
</tr>
<tr>
<td><em>Bodianus frenchii</em></td>
<td>168-169</td>
<td>0.04-0.14</td>
<td>0.38-0.83</td>
</tr>
<tr>
<td><em>Epinephelides armatus</em></td>
<td>198-199</td>
<td>0.21-0.24</td>
<td>0.12-0.17</td>
</tr>
<tr>
<td><em>Epinephelus coioides</em></td>
<td>226-229</td>
<td>0.50-0.54</td>
<td>0.00-0.00</td>
</tr>
<tr>
<td><em>Glaucosoma hebraicum</em></td>
<td>253-255</td>
<td>0.61-0.63</td>
<td>0.00-0.00</td>
</tr>
</tbody>
</table>
**Figure captions**

**Figure S1.** Quantitatively similar somatic growth curves, i.e., curves with AICc scores lying within 2 units of the lowest score (the AICc of the best curve, in black), for *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides* and *Glaucosoma hebraicum*. Pütter = Pütter number 2, VB = traditional von Bertalanffy, ‘a=0, b>0’ = Schnute (1981) growth curve with a = 0 and b > 0, ModVB = modified von Bertalanffy, ND = normal distribution, LND = lognormal distribution.

**Figure S2.** Quantitatively similar otolith growth curves, i.e., curves with AICc scores lying within 2 units of the lowest score (the AICc of the best curve, in black), for *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides* and *Glaucosoma hebraicum*. Pütter = Pütter number 2, VB = traditional von Bertalanffy, GenVB = generalised von Bertalanffy, ‘a=0, b>0’ = Schnute (1981) growth curve with a = 0 and b > 0, ‘a<0, b>0’ = Schnute (1981) growth curve with a < 0 and b > 0, ModVB = modified von Bertalanffy.

**Figure S3.** Relationships between total lengths and otolith radii at age formed by quantitatively similar somatic and otolith growth curves for *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*, *Epinephelus coioides* and *Glaucosoma hebraicum*. Black = best fitting somatic and otolith growth curves. Pütter = Pütter number 2, VB = traditional von Bertalanffy, GenVB = generalised von Bertalanffy, Bertalanffy, ‘a=0, b>0’ = Schnute (1981) growth curve with a = 0 and b > 0, ‘a<0, b>0’ = Schnute (1981) growth curve with a < 0 and b > 0, ModVB = modified von Bertalanffy, ND = normal distribution, LND = lognormal distribution. Quantitatively similar = AICc scores lying within 2 units of the lowest score.
a) Acanthopagrus butcheri

b) Argyrosomus japonicus
c) Bodianus frenchii
d) Epinephelides armatus
e) Epinephelus coioides
f) Glaucosoma hebraicum
a) Acanthopagrus butcheri

- 'a=0, b>0'

b) Argyrosomus japonicus

- 'a=0, b>0'

c) Bodianus frenchii

- 'a=0, b>0'

- ModVB

- 'a<0, b>0'

d) Epinephelides armatus

- VB
- Pütter
- Gompertz
- 'a=0, b>0'
- Logistic
- ModVB

e) Epinephelus coioides

- VB
- 'a=0, b>0'
- ModVB
- GenVB

f) Glaucosoma hebraicum

- ModVB
- 'a<0, b>0'
a) Acanthopagrus butcheri

b) Argyrosomus japonicus

c) Bodianus frenchii

d) Epinephelides armatus

e) Epinephelus coioides

f) Glaucosoma hebraicum