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

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

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Draft

11 *Abstract*

12 Curves describing the length-otolith size relationships for juveniles and adults of six fish
13 species with widely differing biological characteristics were fitted simultaneously to fish
14 length and otolith size at age, assuming that deviations from those curves are correlated rather
15 than independent. The trajectories of the somatic and otolith growth curves throughout life,
16 which reflect changing ratios of somatic to otolith growth rates, varied markedly among
17 species and resulted in differing trends in the relationships formed between fish and otolith
18 size. Correlations between deviations from predicted values were always positive.
19 Dependence of length on otolith growth rate (i.e., 'growth effect') and 'correlated errors in
20 variables' introduce bias into parameter estimates obtained from regressions describing the
21 allometric relationships between fish lengths and otolith sizes. The approach taken in this
22 study to describe somatic and otolith growth accounted for both of these effects and that of
23 age to produce more reliable determinations of the length-otolith size relationships used for
24 back-calculation and assumed when drawing inferences from sclerochronological studies.

25 *Résumé*

26 Les courbes décrivant les relations de longueur-taille de l'otolithe des juvéniles et adultes
27 pour six espèces de poissons, aux caractéristiques biologiques très différentes, ont été ajustées
28 simultanément à la longueur du poisson et à la taille de l'otolithe avec l'âge, en supposant
29 que les déviations de ces courbes sont corrélées plutôt qu'indépendantes. Les trajectoires des
30 courbes de croissance somatique et de l'otolithe tout au long de la vie, qui reflètent les
31 changements de ratios des taux de croissance somatique et de l'otolithe, varièrent de façon
32 marquée entre les espèces et aboutirent à des tendances distinctes dans les relations formées
33 entre la taille des poissons et celle des otolithes. Les corrélations entre les déviations des
34 valeurs estimées étaient toutes positives. La dépendance de la longueur du poisson sur le taux

35 de croissance de l'otolithe (c'est-à-dire, l'effet de croissance) et les “erreurs corrélées dans les
36 variables” introduisent un biais dans les estimations de paramètres obtenues par les
37 régressions décrivant les relations allométriques entre les longueurs de poissons et les tailles
38 des otolithes. L'approche développée dans cette étude pour décrire la croissance somatique et
39 celle de l'otolithe tient compte de ces deux effets, ainsi que celui de l'âge, pour produire une
40 méthode plus fiable de détermination des relations de longueur-taille de l'otolithe, requises
41 dans les études de rétro-calcul et adoptées lors des conclusions tirées dans les études de
42 sclérochronologie.

43 ***Keywords***

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

46 ***Introduction***

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

64 Otoliths are calcified structures used by fish for balance, hearing and orientation (e.g.,
65 Campana and Neilson 1985; Campana 1999; Popper et al. 2005). The growth of these
66 structures, which vary widely in shape and size, is controlled by the combination of two
67 processes: 1) the formation of an organic matrix, regulated by metabolic influences and, thus,
68 to some extent linked to somatic growth; and 2) a physicochemical process, i.e., calcification
69 (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

118 Australian Dhufish *Glaucosoma hebraicum* Richardson, 1845. Maximum ages and lengths
119 for these temperate and subtropical species ranged from ~ 19 to 78 years and from ~ 480 to
120 2 000 mm, respectively¹.

121 The data for *A. butcheri* were derived from samples collected during the present
122 study², whereas those for each of the other species were derived using samples collected in
123 previous studies in Western Australia by staff and research students at Murdoch University.
124 The methods employed and locations from which individuals of each species were collected,
125 are listed in supplemental materials³. Details of the sampling regimes for *A. japonicus*,
126 *B. frenchii*, *E. armatus*, *E. coioides*, and *G. hebraicum* are provided in the associated
127 references describing those respective studies³.

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

130 ***1.2 Fish processing and otolith measurements***

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

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, $g_S(t | S_{\tau_1}, S_{\tau_2}, a_S, b_S)$, which describes size S (either L or R) as a function of age t , where S_{τ_1} and S_{τ_2} are the expected sizes at two specified reference ages τ_1 and τ_2 , and a_S and b_S are parameters that determine the shape of the curve. The minimum and maximum ages at capture of each species were used as the reference ages τ_1 and τ_2 in this study. Thus, the expected length $\hat{L}_j$ of fish j at its age at capture $t_{c,j}$ was calculated as $\hat{L}_j = g_L(t_{c,j} | L_{\tau_1}, L_{\tau_2}, a_L, b_L)$ and the radius of its otolith as $\hat{R}_j = g_R(t_{c,j} | R_{\tau_1}, R_{\tau_2}, a_R, b_R)$. 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:

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

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

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

182 The following four equations comprise the Schnute (1981) model:

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

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

190 Deviations of total length, L , and otolith radius, R , for fish of age t years about the
 191 length $\hat{L}$ and radius $\hat{R}$ predicted by the growth curves for these variables were assumed to be
 192 drawn from one of four candidate bivariate distributions. Thus, for each analysis, for fish j at
 193 its age of capture $t_{c,j}$, the deviations of its recorded values of length L_j and otolith radius
 194 R_j from the expected values for fish of that age were drawn from either the bivariate normal,
 195 normal-lognormal, lognormal-normal, or bivariate lognormal distributions. The form of this
 196 distribution determines the forms of the associated marginal distributions for the deviations of
 197 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., $L_j = \hat{L}_j + \varepsilon_j$ or $R_j = \hat{R}_j + \eta_j$, or lognormal distributions, i.e., $L_j = \hat{L}_j \exp(\varepsilon_j)$ or $R_j = \hat{R}_j \exp(\eta_j)$, where, in each case, the correlation between values of ε and η is ρ .

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

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

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

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

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

$$(L_j, R_j) \sim \text{LNN}(\ln(\hat{L}_j) - \sigma_\varepsilon^2/2, \hat{R}_j, \sigma_\varepsilon^2, \sigma_\eta^2, \rho), \text{ or}$$

(4) a bivariate lognormal distribution, where

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

and where the probability density functions for these distributions are presented in the supplemental materials⁶. 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 $L_j = \hat{L}_j \exp(\varepsilon_j)$ 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

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 magnitudes⁷.

The parameters estimated for each bivariate model were those for the somatic growth equation, i.e., L_{τ_1} , L_{τ_2} , a_L , b_L , and s_ε , those for the otolith growth equation, i.e., R_{τ_1} , R_{τ_2} , a_R , b_R , and s_η , and the correlation ρ of the bivariate distribution. Note also that s_ε and s_η are estimates of the standard deviations σ_ε and σ_η , 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_{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.,

Hoffman 2001). 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*⁸. 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 model⁹. For *A. butcheri*, the AICc scores of the

⁸ Table S5

⁹ Table S6

291 traditional von Bertalanffy, Gompertz curve and logistic curves, all with normally distributed
292 deviations, lay close to and within 2 units of that of the Pütter number 2 curve¹⁰. For
293 *A. japonicus* and *E. coioides*, the AICc scores of the Pütter number 2 curve approached those
294 (and within 2 units) of the traditional von Bertalanffy curves. The modified von Bertalanffy
295 curve, with the lognormal distribution, provided a description of the lengths at age of
296 *B. frenchii* that was of similar quality (and with an AICc that differed by < 2 units) to that
297 produced by the same curve with normally-distributed deviations. The quantitatively similar
298 lengths at age predicted for the different species by those somatic growth curves with AICc
299 scores exceeding those of the best models by < 2 units differed only slightly from the values
300 calculated using those latter models, with differences most evident at the ends of the age
301 ranges or, within those ranges, where data were sparse¹¹.

302 ***Forms of growth curves providing best descriptions of otolith radius at age***

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

¹⁰ Table S6

¹¹ Fig. S1

314 ~ 4 years of age, the radii continued to increase, approximately linearly, with age over the
315 remainder of the age range of the sample. The same growth curves were identified using
316 AICc and the bootstrapping procedure (Table 2).

317 For *B. frenchii*, the modified von Bertalanffy and a Schnute (1981) curve with $a < 0$
318 and $b > 0$ differed by less than 2 units from the AICc best model¹². The AICc scores of the
319 Pütter number 2, the Gompertz, a Schnute (1981) curve with $a = 0$ and $b > 0$, the logistic, and
320 the modified von Bertalanffy curves describing otolith size at age of *E. armatus* were similar
321 to the traditional von Bertalanffy curve identified as best representing those otolith sizes at
322 age. For *E. coioides*, the AICc scores of the Schnute (1981) curve with $a = 0$ and $b > 0$, the
323 modified and the generalised von Bertalanffy curves were within 2 units of the traditional von
324 Bertalanffy curve. A Schnute (1981) model with parameters $a < 0$ and $b > 0$ provided another
325 alternative model with a quantitatively similar description of otolith growth for *G. hebraicum*.
326 As with the somatic growth curves, differences for each species between the otolith radii at
327 age predicted by the models with AICc scores exceeding that of the best model by < 2 units
328 and the values predicted by that latter model differed only slightly and mainly at the ends of
329 the age range or, within that range, where data were sparse¹³.

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

331 The somatic growth curves for *A. butcheri*, *A. japonicus*, *B. frenchii* and *E. coioides*
332 that employed a normal rather than lognormal marginal distribution provided the best
333 description of the deviations of observed lengths at age from the values predicted by the
334 growth curve (Table 1). For both *E. armatus* and *G. hebraicum*, however, lognormal
335 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_{adjusted} was 0.79 (Table 3; Fig. 1)¹⁴. 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 ~ 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., ~ 30 years for *A. japonicus* and ~ 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

¹⁴ Table S9

For the five species for which R^2_{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. 2d)¹⁵.

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 ~ 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 ~ 2 years, was reduced from age ~ 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

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 sparse¹⁷.

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., Beamesderfer and Rieman 1988; Arreguín-Sánchez 1996; Helidoniotis and Haddon 2013).

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 years¹⁹. 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.

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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.

Species	Somatic growth			Otolith growth		
	Curve type	Error type	AW (%)	Curve type	Error type	AW (%)
<i>Acanthopagrus butcheri</i>	Pütter number 2	normal	24	$a = 0$ and $b > 0$	lognormal	48
<i>Argyrosomus japonicus</i>	Traditional von Bertalanffy	normal	38	$a = 0$ and $b > 0$	lognormal	62
<i>Bodianus frenchii</i>	Modified von Bertalanffy	normal	47	$a = 0$ and $b > 0$	lognormal	38
<i>Epinephelides armatus</i>	Logistic	lognormal	37	Traditional von Bertalanffy	lognormal	20
<i>Epinephelus coioides</i>	Traditional von Bertalanffy	normal	46	Traditional von Bertalanffy	normal	25
<i>Glaucosoma hebraicum</i>	$a = 0$ and $b > 0$	lognormal	48	Modified von Bertalanffy	lognormal	48

845

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.

Species	Somatic growth			Otolith growth		
	Curve type	Error type	Bootstrap percentage (%)	Curve type	Error type	Bootstrap percentage (%)
<i>Acanthopagrus butcheri</i>	Traditional von Bertalanffy	normal	36	$a = 0$ and $b > 0$	lognormal	81
<i>Argyrosomus japonicus</i>	Traditional von Bertalanffy	normal	32	$a = 0$ and $b > 0$	lognormal	85
<i>Bodianus frenchii</i>	Modified von Bertalanffy	normal	85	$a = 0$ and $b > 0$	lognormal	60
<i>Epinephelides armatus</i>	Logistic	lognormal	74	Traditional von Bertalanffy	lognormal	33
<i>Epinephelus coioides</i>	Traditional von Bertalanffy	normal	65	Traditional von Bertalanffy	normal	41
<i>Glaucosoma hebraicum</i>	$a = 0$ and $b > 0$	lognormal	67	Modified von Bertalanffy	lognormal	75

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. τ_1 = first reference age (youngest fish in the sample), τ_2 = second reference age (oldest fish in the sample), a and b = parameters of growth model, y_1 = size at age τ_1 , y_2 = size at age τ_2 . Standard errors (SE) of the parameters and of the standard deviations are presented in parentheses.

Species	Growth type	a	b	y_1	y_2	SD
<i>Acanthopagrus butcheri</i> ($\tau_1 = 0.62$, $\tau_2 = 19.62$)	Somatic	0.19 (SE = 0.02)	0.33	98 (SE = 6.69)	327 (SE = 7.25)	17 (SE = 1.67)
	Otolith	0	2.03 (SE = 0.16)	0.41 (SE = 0.01)	1.65 (SE = 0.04)	0.06 (SE = 0.01)
<i>Argyrosomus japonicus</i> ($\tau_1 = 0.22$, $\tau_2 = 31.03$)	Somatic	0.24 (SE = 0.02)	1	154 (SE = 39.37)	1214 (SE = 27.21)	79 (SE = 7.92)
	Otolith	0	1.64 (SE = 0.05)	0.57 (SE = 0.05)	10.21 (SE = 0.30)	0.09 (SE = 0.01)
<i>Bodianus frenchii</i> ($\tau_1 = 1.13$, $\tau_2 = 61.91$)	Somatic	0.28 (SE = 0.05)	-0.38 (SE = 0.53)	90 (SE = 15.42)	420 (SE = 12.55)	21 (SE = 2.07)

	Otolith	0	1.78 (SE = 0.16)	0.36 (SE = 0.02)	2.09 (SE = 0.08)	0.09 (SE = 0.01)
<hr/>						
<i>Epinephelides armatus</i> ($\tau_1 = 1.71, \tau_2 = 13.04$)	Somatic	0.38 (SE = 0.05)	-1	149 (SE = 9.75)	482 (SE = 21.85)	0.11 (SE = 0.01)
	Otolith	0.33 (SE = 0.08)	1	0.52 (SE = 0.04)	1.06 (SE = 0.04)	0.10 (SE = 0.01)
<hr/>						
<i>Epinephelus coioides</i> ($\tau_1 = 0.15, \tau_2 = 14.70$)	Somatic	0.12 (SE = 0.02)	1	70 (SE = 19.55)	1059 (SE = 29.36)	61 (SE = 6.13)
	Otolith	0.15 (SE = 0.02)	1	0.35 (SE = 0.03)	1.87 (SE = 0.05)	0.11 (SE = 0.01)
<hr/>						
<i>Glaucosoma hebraicum</i> ($\tau_1 = 0.71, \tau_2 = 24.20$)	Somatic	0	1.90 (SE = 0.19)	105 (SE = 7.79)	992 (SE = 43.73)	0.12 (SE = 0.01)
	Otolith	1.31 (SE = 0.38)	0.22 (SE = 0.16)	0.74 (SE = 0.04)	3.42 (SE = 0.12)	0.09 (SE = 0.01)

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 ρ 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.

Species	NLL	ρ	$P\{\rho > 0\}$	Prop. of bootstraps > 0
<i>Acanthopagrus butcheri</i>	141	0.31 (SE = 0.13)	0.04	0.97
<i>Argyrosomus japonicus</i>	299	0.13 (SE = 0.14)	0.43	0.89
<i>Bodianus frenchii</i>	169	0.06 (SE = 0.14)	0.73	0.64
<i>Epinephelides armatus</i>	199	0.22 (SE = 0.13)	0.15	0.95
<i>Epinephelus coioides</i>	228	0.50 (SE = 0.11)	0.00	1
<i>Glaucosoma hebraicum</i>	253	0.63 (SE = 0.09)	0.00	1

867

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*.

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279x384mm (300 x 300 DPI)

1 **Supplemental materials for Ashworth *et al.* CJFAS**

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

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

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7 **References for Table S1**

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

58 *Acanthopagrus butcheri* was sampled in the Wellstead Estuary at 34°50'S latitude and
59 118°60'E longitude on the south coast of Western Australia in May 2013 using seine and gill
60 nets. The seine net was 21.5 m long and comprised two 10 m long wings (6 m of 9 mm mesh
61 and 4 m of 3 mm mesh) and a 1.5 m wide bunt of 3 mm mesh. This net, which was deployed
62 during daylight, fished to a depth of ~ 1.5 m and swept an area of ~ 116 m². The sunken
63 composite multifilament gill net comprised seven 20 m long panels, each with a height of 2 m
64 and containing a different stretched mesh size, i.e., 51, 63, 76, 89, 102, 115 or 127 mm mesh.
65 Gill nets were set parallel to the shore at dusk and retrieved ~ 2 to 3 h later. Fish were
66 euthanized in an ice slurry immediately after capture and transported to the laboratory where
67 they were frozen until processed.

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

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

71

72 **References for Table S2**

73 Cossington, S., Hesp, S. A., Hall, N. G., and Potter, I. C. 2010. Growth and reproductive biology of the foxfish
74 *Bodianus frenchii*, a very long-lived and monandric protogynous hermaphroditic labrid. J. Fish
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77 parameters required for managing the fisheries for mullet and silver trevally in Western Australia.
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83 management of this species. Fish. Bull. **100**(2): 214-227.
- 84 Moore, S. E., Hesp, S. A., Hall, N. G., and Potter, I. C. 2007. Age and size compositions, growth and
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91 http://frdc.com.au/research/Final_Reports/2002-003-DLD.PDF [accessed 17 October 2014].

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

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

95

96 **References for Table S3**

97 Cossington, S., Hesp, S. A., Hall, N. G., and Potter, I. C. 2010. Growth and reproductive biology of the foxfish
98 *Bodianus frenchii*, a very long-lived and monandric protogynous hermaphroditic labrid. J. Fish
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100 Farmer, B. 2008. Comparisons of the biological and genetic characteristics of the Mulloway *Argyrosomus*
101 *japonicus* (Sciaenidae) in different regions of Western Australia. PhD thesis, School of Biological
102 Sciences and Biotechnology. Murdoch University, Western Australia. Available from
103 <http://researchrepository.murdoch.edu.au/id/eprint/682> [accessed 17 October 2014].

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- 107 Moore, S. E., Hesp, S. A., Hall, N. G., and Potter, I. C. 2007. Age and size compositions, growth and
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116 (Sparidae) among estuaries: some possible contributing factors. Fish. Bull. **98**(4): 785-799.

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

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

123 The **generalised von Bertalanffy growth curve**, obtained by setting values of $a > 0$ and
124 $b > 0$ in the Schnute model, may be written as

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

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

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

$$Y(t) = y_{\infty} \left(1 - \frac{1}{p} \exp[-g(t - t_0)] \right)^{-p} \tag{2}$$

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

$$Y(t) = y_{\infty} \exp(-\exp[-g(t - t_0)]) \tag{3}$$

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

$$Y(t) = y_{\infty}(1 + \exp[-g(t - t_0)])^{-1} \tag{4}$$

133

134

135 The **linear growth curve**, obtained using values of $a = 0$ and $b = 1$, is

$$Y(t) = g(t - t_0) \quad (5)$$

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

$$Y(t) = (\alpha + \beta t)^2 \quad (6)$$

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

138 is

$$Y(t) = \alpha \beta^t \quad (7)$$

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

140 $\gamma > 0$, is

$$Y(t) = \alpha + \beta \exp(\gamma t) \quad (8)$$

141

142 **Reference for Supplemental material S2**

143 Schnute, J. 1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. **38**(9):

144 1128-1140. doi: 10.1139/f81-153.

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

Region	Parameter space
1	$a > 0$ and $b > 0$
2	$a > 0$ and $b < 0$
3	$a < 0$ and $b > 0$
4	$a < 0$ and $b < 0$
5	$a > 0$ and $b = 0$
6	$a < 0$ and $b = 0$
7	$a = 0$ and $b > 0$
8	$a = 0$ and $b < 0$
9	$a = 0$ and $b = 0$

150

151 **Note.** Several regions described in this table, and defined by the constraints imposed on the
152 parameters a and b , were the same as those of the specific common growth curves described
153 by Schnute (1981), i.e., the Region 1 curve (above) is equivalent to the generalized von
154 Bertalanffy curve, the Region 2 curve is equivalent to the Richards growth curve, the Region
155 5 curve is equivalent to the Gompertz growth curve and the Region 9 curve is equivalent to
156 the t^{th} power curve¹.

¹ Supplemental material S2

157 **Reference for Table S4**

- 158 Schnute, J. 1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. **38**(9):
159 1128-1140. doi: 10.1139/f81-153.

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160 **Supplemental material S3. Univariate and bivariate probability density functions**

161 **Univariate normal distribution**

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

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

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

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

165 **Univariate lognormal distribution**

166 If y has a lognormal distribution with mean μ and standard deviation σ , i.e.,
 167 $y \sim \text{LN}(\mu, \sigma^2)$, the probability density function (Burnham and Anderson 2002) may be written
 168 as

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

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

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

170 **Bivariate normal distribution**

171 If y_1 and y_2 have a bivariate normal distribution with means of μ_1 and μ_2 ,
 172 respectively, and standard deviations σ_1 and σ_2 , respectively, and with correlation coefficient

173 ρ , i.e., $(y_1, y_2) \sim \text{BVN}(\mu_1, \mu_2, \sigma_1^2, \sigma_2^2, \rho)$, then the probability density function of the joint
 174 distribution of these two variables is

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

175 where

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

$$A = \frac{y_1 - \mu_1}{\sigma_1}$$

176 and

$$B = \frac{y_2 - \mu_2}{\sigma_2}$$

177 The negative log-likelihood of observed pairs of values y_{1j} and y_{2j} , where $j = 1, 2, \dots, n$,
 178 may be calculated as

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

179 The conditional distribution of y_1 given y_2 is the normal distribution with:

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

181 **Bivariate lognormal distribution**

182 If y_1 and y_2 have a bivariate lognormal distribution (e.g., Cheng 1986) with means of
 183 μ_1 and μ_2 , respectively, and standard deviations σ_1 and σ_2 , respectively, and with correlation
 184 coefficient ρ , 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
 185 the joint distribution of these two variables is

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

186 where

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

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

187 and

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

188 The negative log-likelihood of observed pairs of values y_{1j} and y_{2j} , where $j = 1, 2, \dots, n$,

189 may be calculated as

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

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

$$191 \quad y_1 \sim \text{LN} \left(\mu_1 + \rho \frac{\sigma_1}{\sigma_2} (\ln(y_2) - \mu_2), \sigma_1^2 (1 - \rho^2) \right),$$

192 where the probability density function of this distribution is

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

193

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 μ_1 and standard deviations σ_1 and y_2 has a lognormal distribution with mean of μ_2 and standard deviations σ_2 , and with correlation coefficient between y_1 and $\ln(y_2)$ of ρ , i.e., $(y_1, y_2) \sim NLN(\mu_1, \mu_2, \sigma_1^2, \sigma_2^2, \rho)$, 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

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

$$A = \frac{y_1 - \mu_1}{\sigma_1}$$

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 $j = 1, 2, \dots, n$, may be calculated as

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

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.

207 The conditional distribution of y_1 , given y_2 , is the normal distribution with:

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

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

210 $y_2 \sim \text{LN} \left(\mu_2 + \rho \frac{\sigma_2}{\sigma_1} (y_1 - \mu_1), \sigma_2^2 (1 - \rho^2) \right)$,

211 where the probability density function of this lognormal distribution is:

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

212

213 **Reference for Supplemental material S3**

214 Burnham, K. P., and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-
215 theoretic approach. Springer. Science and Business Media. ISBN: 0-387-95364-7.

216 Cheng, Y. S. 1986. Bivariate lognormal distribution for characterizing asbestos fiber aerosols. Aerosol Sci.
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218 Chen, D. G., and Holtby, L. B. 2002. A regional meta-model for stock-recruitment analysis using an empirical
219 Bayesian approach. Can. J. Fish. Aquat. Sci. **59**(9): 1503-1514. doi: 10.1139/f02-118.

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.

Curve type	Normal distribution		Lognormal distribution	
	AICc	AW	AICc	AW
Modified von Bertalanffy	434.70	0.01	442.64	< 0.01
Generalised von Bertalanffy	434.57	0.07	442.61	< 0.01
Traditional von Bertalanffy	432.22	0.23	440.17	< 0.01
Pütter number 2	432.19	0.24	440.57	< 0.01
Gompertz	432.46	0.21	441.25	< 0.01
Richards	434.94	0.06	443.73	< 0.01
Logistic	433.92	0.10	444.44	< 0.01
Linear	489.04	0.00	493.38	0.00
Quadratic	500.87	0.00	515.23	0.00
t th power	509.73	0.00	532.14	0.00
Exponential	491.46	0.00	495.81	0.00
a < 0 and b > 0	441.08	< 0.01	448.27	0.00
a < 0 and b < 0	514.61	0.00	591.94	0.00
a < 0 and b = 0	512.13	0.00	534.55	0.00
a = 0 and b > 0	438.60	0.01	445.79	< 0.01
a = 0 and b < 0	512.10	0.00	534.51	0.00

Note. Bold font is used to identify the growth curve with the lowest AICc.

228 **Reference for Table S5**

229 Schnute, J. 1981. A versatile growth model with statistically stable parameters. *Can. J. Fish. Aquat. Sci.* **38**(9):
230 1128-1140. doi: 10.1139/f81-153.

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

Species	Curve type	Distribution type	AICc
<i>Acanthopagrus butcheri</i>	Pütter number 2	normal	432.19
	Traditional von Bertalanffy	normal	432.22
	Gompertz	normal	432.46
	Logistic	normal	433.92
<i>Argyrosomus japonicus</i>	Traditional von Bertalanffy	normal	587.93
	Pütter number 2	normal	589.12
<i>Bodianus frenchii</i>	Modified von Bertalanffy	normal	456.11
	Modified von Bertalanffy	lognormal	456.25
<i>Epinephelides armatus</i>	Logistic	lognormal	508.08
<i>Epinephelus coioides</i>	Traditional von Bertalanffy	normal	562.38
	Pütter number 2	normal	564.37
<i>Glaucosoma hebraicum</i>	$a = 0$ and $b > 0$	lognormal	564.78

236

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.

Curve type	Normal distribution		Lognormal distribution	
	AICc	AW	AICc	AW
Modified von Bertalanffy	-115.79	< 0.01	-123.51	0.09
Generalised von Bertalanffy	-115.94	< 0.01	-124.48	0.14
Traditional von Bertalanffy	-118.26	0.01	-123.87	0.10
Pütter number 2	-117.34	< 0.01	-120.02	0.02
Gompertz	-116.62	< 0.01	-117.84	< 0.01
Richards	-114.15	< 0.01	-115.37	< 0.01
Logistic	-113.80	< 0.01	-111.33	< 0.01
Linear	-87.04	0.00	-88.83	0.00
Quadratic	-67.23	0.00	-57.83	0.00
t th power	-52.15	0.00	-32.88	0.00
Exponential	-84.60	0.00	-86.39	0.00
a < 0 and b > 0	-115.45	< 0.01	-124.56	0.15
a < 0 and b < 0	-47.25	0.00	47.22	0.00
a < 0 and b = 0	-49.73	0.00	-30.46	0.00
a = 0 and b > 0	-117.93	0.01	-126.95	0.48
a = 0 and b < 0	-49.78	0.00	-30.51	0.00

Note. Bold font is used to identify the growth curve with the lowest AICc.

245 **Reference for Table S7**

- 246 Schnute, J. 1981. A versatile growth model with statistically stable parameters. *Can. J. Fish. Aquat. Sci.* **38**(9):
247 1128-1140. doi: 10.1139/f81-153.

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

Species	Curve type	Distribution type	AICc
<i>Acanthopagrus butcheri</i>	$a = 0$ and $b > 0$	lognormal	-126.95
<i>Argyrosomus japonicus</i>	$a = 0$ and $b > 0$	lognormal	29.49
<i>Bodianus frenchii</i>	$a = 0$ and $b > 0$	lognormal	-97.07
	Modified von Bertalanffy	lognormal	-96.35
	$a < 0$ and $b > 0$	lognormal	-95.82
<i>Epinephelides armatus</i>	Traditional von Bertalanffy	lognormal	-91.97
	Pütter number 2	lognormal	-91.77
	Gompertz	lognormal	-91.64
	$a = 0$ and $b > 0$	lognormal	-91.24
	Logistic	lognormal	-91.21
	Modified von Bertalanffy	lognormal	-90.63
<i>Epinephelus coioides</i>	Traditional von Bertalanffy	normal	-74.41
	$a = 0$ and $b > 0$	normal	-74.31
	Modified von Bertalanffy	normal	-74.20
	Generalised von Bertalanffy	normal	-73.77
<i>Glaucosoma hebraicum</i>	Modified von Bertalanffy	lognormal	-13.15
	$a < 0$ and $b > 0$	lognormal	-11.36

253

Table S9. Values of adjusted coefficients of determination (R^2_{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.

Species	R^2_{adjusted}	
	Total length	Otolith radius
<i>Acanthopagrus butcheri</i>	0.92	0.94
<i>Argyrosomus japonicus</i>	0.92	0.96
<i>Bodianus frenchii</i>	0.91	0.94
<i>Epinephelides armatus</i>	0.79	0.53
<i>Argyrosomus japonicus</i>	0.95	0.94
<i>Glaucosoma hebraicum</i>	0.88	0.87

260

261 **Table S10.** Ranges of negative log-likelihoods (NLL) for the bivariate growth models
262 produced using the quantitatively similar somatic and otolith growth curves for
263 *Acanthopagrus butcheri*, *Argyrosomus japonicus*, *Bodianus frenchii*, *Epinephelides armatus*,
264 *Epinephelus coioides* and *Glaucosoma hebraicum*, together with ranges of both the
265 correlations (ρ) between deviations from the growth curves for those bivariate models and the
266 P-values, $P\{\rho > 0\}$, of one-tailed t-tests that those correlations exceed zero. Quantitatively
267 similar curves were those with AICc scores lying within 2 units of the lowest score, i.e., the
268 AICc of the fitted curve that best described the data.

Species	NLL	ρ	$P\{\rho > 0\}$
<i>Acanthopagrus butcheri</i>	141-142	0.31-0.31	0.04-0.05
<i>Argyrosomus japonicus</i>	299-300	0.12-0.13	0.42-0.45
<i>Bodianus frenchii</i>	168-169	0.04-0.14	0.38-0.83
<i>Epinephelides armatus</i>	198-199	0.21-0.24	0.12-0.17
<i>Epinephelus coioides</i>	226-229	0.50-0.54	0.00-0.00
<i>Glaucosoma hebraicum</i>	253-255	0.61-0.63	0.00-0.00

269

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, '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.