

Abstract—Fish growth is commonly estimated from length-at-age data obtained from otoliths. There are several techniques for estimating length-at-age from otoliths including 1) direct observed counts of annual increments; 2) age adjustment based on a categorization of otolith margins; 3) age adjustment based on known periods of spawning and annuli formation; 4) back-calculation to all annuli, and 5) back-calculation to the last annulus only. In this study we compared growth estimates (von Bertalanffy growth functions) obtained from the above five methods for estimating length-at-age from otoliths for two large scombrids: narrow-barred Spanish mackerel (*Scomberomorus commerson*) and broad-barred king mackerel (*Scomberomorus semifasciatus*). Likelihood ratio tests revealed that the largest differences in growth occurred between the back-calculation methods and the observed and adjusted methods for both species of mackerel. The pattern, however, was more pronounced for *S. commerson* than for *S. semifasciatus*, because of the pronounced effect of gear selectivity demonstrated for *S. commerson*. We propose a method of substituting length-at-age data from observed or adjusted methods with back-calculated length-at-age data to provide more appropriate estimates of population growth than those obtained with the individual methods alone, particularly when faster growing young fish are disproportionately selected for. Substitution of observed or adjusted length-at-age data with back-calculated length-at-age data provided more realistic estimates of length for younger ages than observed or adjusted methods as well as more realistic estimates of mean maximum length than those derived from back-calculation methods alone.

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Integrating methods for determining length-at-age to improve growth estimates for two large scombrids

Aaron C. Ballagh (contact author)^{1,*}

David Welch^{1,2}

Ashley J. Williams^{1,3}

Amos Mapleston¹

Andrew Tobin¹

Nicholas Marton⁴

Email address for contact author: aaron.ballagh@jcu.edu.au

¹ Fishing and Fisheries Research Centre
School of Earth and Environmental Sciences
James Cook University
Townsville, Queensland 4811, Australia

*Present address for contact author: Research Services
James Cook University
Townsville, Queensland 4811 Australia

² Queensland Primary Industries
and Fisheries
Department of Employment, Economic
Development and Innovation
P.O. Box 1085
Oonoonba, Queensland 4811, Australia

³ Oceanic Fisheries Programme
Secretariat of the Pacific Community BP D5
98848 Noumea CEDEX, New Caledonia

⁴ Australian Bureau of Agricultural and
Resource Economics—Bureau of Rural Sciences
Department of Agriculture, Fisheries and Forestry
GPO Box 1563
Canberra, Australian Capital Territory 2601, Australia

Growth is perhaps the most studied of all parameters used to describe the life history of exploited fish. Growth is usually expressed as a mathematical equation describing the mean growth of a population and relating size to age (Katsanevakis and Maravelias, 2008). An understanding of growth is fundamental for population modeling, stock assessments, and managing exploited species (Gulland, 1988). The methods used to estimate growth in fish vary significantly with the type of data being used. The most commonly used data for estimating fish growth is length-at-age data, although length-frequency data and mark-recapture data are also used (Francis, 1988; Labelle et al., 1993). Counts of periodic growth increments observed in otoliths or other hard parts are predominantly used to estimate fish age (Begg et al., 2005; Campana, 2005), and a range of growth models have been developed to be fitted to length-at-age data (e.g., Ricker, 1979; Schnute, 1981). However, length-at-

age estimates are not always collected or treated in the same way, either because of sampling bias or differences in aging protocols, and it is often unknown to what degree differences in length-at-age estimation methods affect parameter estimates from growth models.

Obtaining length-at-age data from otoliths is not always as simple as counting the number of growth increments (Francis et al., 1992; Campana, 2001), and many methods have been used to obtain length-at-age data such as image analysis (e.g., Fablet, 2006), back-calculation (e.g., Campana, 1990; Secor and Dean, 1992), otolith weight and morphometric relationships (e.g., Lou et al., 2005; Steward et al., 2009), length-mediation (e.g., Francis et al., 2005), and age adjustment (e.g., DeVries and Grimes, 1997; Williams et al., 2005; Williams et al., 2008). A combination of methods have been used in studies to estimate growth, where methods such as

back-calculation allow the estimation of lengths-at-ages that are rarely observed, particularly in the absence of a representative sample because of gear selectivity (Lopez-Abellan et al., 2008), or to increase the amount of length-at-age data to be used in fitting a growth curve (e.g., Shafi and Jasim, 1982; Grudtsev and Korolevich, 1986).

Temporal and spatial variation in growth can have significant implications for the assessment and management of exploited populations (Rahikainen and Stephenson, 2004). However, variation in growth from estimation error is also likely to have significant implications for stock assessment, and accounting for bias in growth estimation is not always feasible (Gwinn et al., 2010). Substantial differences in growth estimates have previously been demonstrated from different methods for determining length-at-age from otoliths and other hard parts (e.g., Lucena and O'Brien, 2001; Ballagh et al., 2006). We examine the effects of several different methods for determining length-at-age from otoliths.

Here we compared estimates of growth derived from several commonly used methods for obtaining length-at-age data from otoliths. We applied this approach to the otoliths of two large scombrids, narrow-barred Spanish mackerel (*Scomberomorus commerson*) and broad-barred king mackerel (*Scomberomorus semifasciatus*), to test for differences in growth attributable to the methods used, and to make inferences about which method(s) provides the most appropriate estimate of length-at-age for growth estimation. *Scomberomorus commerson* and *S. semifasciatus* are fast growing species and it was expected that differences in growth estimates from different length-at-age data would be clearer than those for slower growing species. We also examined the effects on growth estimates when length-at-age data from different methods are combined, such as when back-calculated and observed length-at-age data are combined (e.g., Lopez-Abellan et al., 2008).

Materials and methods

Samples of *S. commerson* were collected from several locations along the east coast of Queensland from commercial and recreational fishermen using various hook-and-line gears, and *S. semifasciatus* samples were collected from the east coast of Queensland, Gulf of Carpentaria, and the Northern Territory from commercial fishermen using gillnets of various mesh sizes. A small number of juveniles of each species were collected by beam trawl from the east coast of Queensland.

Length-at-age and growth

For each mackerel species five methods of determining length-at-age from otoliths were investigated: observed (Obsv); category-adjusted (Adj-cat); formula-adjusted (Adj-frm); back-calculation to all annuli (BC-all); and back-calculation to the last annulus only (BC-last).

Table 1

Description of otolith margin categories used in age adjustment of *Scomberomorus commerson* and *S. semifasciatus*.

Margin category	Description
0	Complete and continuous opaque band formed around edge of otolith, and no translucent material beyond the last opaque band
I	Translucent band laid onto the outer edge comprising 1/4–1/3 the width of the previous translucent band
II	Translucent band laid onto outer edge comprising roughly 1/2 the width of the previous translucent band
III	Opaque band present on edge; however, is not continuous or complete

Otoliths were aged, measured, and back-calculation of previous length-at-age for both species was done by using identical methods (Ballagh et al., 2006; Tobin and Mapleston¹; Welch et al.²). Observed length-at-age was defined as the agreed upon count of complete opaque increments (annuli) from multiple readings (up to three) of each otolith, coupled with the fork length of the fish at capture. Back-calculation of previous length-at-age was done by using the body proportional hypothesis described by Francis (1990) with the parameters from linear geometric mean regression of otolith radius on fork length (e.g., Ballagh et al., 2006).

Two methods for age adjustment were investigated in this study: category adjustment, and formula adjustment. Category adjustment was based on simple criteria whereby the observed age of each otolith was adjusted for the marginal increment at the outer edge of the otolith, which was categorized according to a system (margin category, Table 1, Fig. 1). Otoliths for which there was agreement in the annuli count were assigned a final margin category if any two of the margin categories from multiple readings for a single otolith were the same. For final margin categories of 0 or I, no age adjustment was deemed necessary and the agreed upon count of annuli was accepted as the

¹ Tobin, A. J., and A. Mapleston. 2004. Exploitation dynamics and biological characteristics of the Queensland East Coast Spanish mackerel (*Scomberomorus commerson*) fishery. CRC Reef Research Centre Technical Report No 51, 61 p. CRC Reef Research Centre, Townsville, Australia.

² Welch, D. J., R. C. Buckworth, J. R. Oviden, S. J. Newman, D. Broderick, R. J. G. Lester, A. C. Ballagh, J. M. Stapley, R. A. Charters, and N. A. Gribble. 2009. Determination of management units for grey mackerel fisheries in northern Australia. Final Report, Fisheries Research and Development Corporation Project 2005/010. Fishing and Fisheries Research Centre Technical Report No. 4, 158 p. Fishing and Fisheries Research Centre, James Cook University, Townsville, Australia.

final age because marginal increment growth beyond a complete annulus, and thus a whole year, was considered to be negligible. Final margin categories of II were considered to be closer to half a complete annulus, and thus the equivalent of growth for half a year, and therefore the age was adjusted by adding 0.5 to the count of annuli to give the final age. For otoliths with a final margin category of III, the marginal increment was considered to be close to a whole annulus and therefore the age was adjusted by adding one to the agreed upon count of annuli. For otoliths with margin categories that were not the same, the higher of the category estimates was accepted as the final margin category and age was adjusted accordingly.

For otoliths with no agreed upon age, it was still possible to assign an adjusted age in some cases on the basis of the margin increment category and the age estimates. If multiple age estimates were no more than one year apart, the margin category of the higher age was 0 or I, and the margin category for the lower age estimate was III, the adjusted age was accepted as the higher of the two age estimates. If there was still no agreement between readings on ages and margin categories, the otolith was rejected for age adjustment. Less than 0.5% of all otoliths were rejected for age adjustment.

Formula adjustment was based on a modification of the age adjustment algorithms used in Williams et al. (2008). The age adjustment formula corrected for the collection of samples across different months of the year by adjusting observed-age estimates to account for the period of annuli formation, spawning period (birth date), and the date of capture. The following algorithms were used to adjust age estimates:

$$\text{If } N = 0, \text{ age}_m = m_c, \quad (1)$$

$$\text{If } N > 0, \text{ age}_m = ((N - 1) \times 12) + m_b + m_c, \quad (2)$$

where N = number of complete annuli;

age_m = age in months;

m_b = number of months from the assigned birth date to the assigned date of annuli formation; and

m_c = number of months from the assigned date of annuli formation to the date of capture.

It was inferred from previous studies that the period of annuli formation coincides with the spawning period for both species (McPherson, 1992, 1993; Tobin and Mapleston¹; Welch et al.²; Cameron and Begg³). The birth date and date of annulus completion was

³ Cameron, D., and G. Begg. 2002. Fisheries biology and interaction in the northern Australian small mackerel fishery. Final report to the Fisheries Research and Development Corporation, projects 92/144 and 92/144.02, 236 p. Department of Primary Industries, Brisbane, Queensland, Australia.

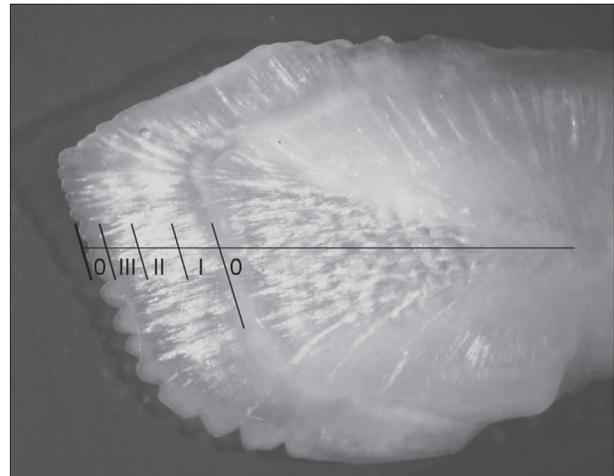


Figure 1

Otolith of narrow-barred Spanish mackerel (*Scomberomorus commerson*), showing the margin categories used in age adjustment (see Table 1). In this example a complete opaque band (annulus) is visible at the otolith margin (margin category=0, adjusted age=2).

assigned as 1 November, which represents the mid spawning period for both species (McPherson, 1993; Welch et al.²; Cameron and Begg³). As a result, the time between spawning (birth date) and the timing of annuli formation (m_b) was assigned as 12 months.

All analyses were done separately for females and males as previous studies have shown both species have sexually dimorphic growth (McPherson, 1992; Ballagh et al., 2006; Welch et al.²; Cameron and Begg³). The von Bertalanffy growth function (VBGF, Beverton and Holt, 1957) was used to describe the growth of both species for all length-at-age data and is described by the following equation:

$$L_t = L_\infty (1 - e^{-K(t-t_0)}), \quad (3)$$

where L_t = length at age t ;

L_∞ = theoretical maximum length;

K = growth coefficient or the rate at which L_∞ is asymptotically reached; and

t_0 = theoretical age where length is equal to zero.

VBGF curves were fitted to length-at-age data by non-linear regression. Likelihood ratio tests (Kimura, 1980) were used to test for differences in growth among the different methods for estimating length-at-age for both species. Likelihood ratio tests were used to test for overall differences in growth (all parameters assumed equal), as well as differences in individual parameters of the VBGF. Data were truncated for all likelihood ratio tests so that equivalent age ranges were compared (Haddon, 2001). Where differences were found, multiple comparisons were performed by using likelihood

ratio tests on pairs of individual methods. A Bonferroni adjustment was used for the multiple comparisons to account for inflation in the probability of a type-I error by adjusting the significance level:

$$\alpha_{adj} = \frac{\alpha}{n}, \quad (4)$$

where α = significance level;

α_{Adj} = adjusted significance level; and
 n = number of multiple comparisons.

Selectivity effects

Mean back-calculated length-at-age from all annuli was compared to mean back-calculated length-at-age from the last annulus to infer if there were any selectivity effects that had biased the sample of each species, or if Lee's phenomenon (Ricker, 1969) was present. Lee's phenomenon, whereby lengths at early ages back-calculated from younger fish are greater than lengths at the same age estimated from older fish, has been shown to bias estimates of growth based on back-calculation of length-at-age by using all annuli (Vaughan and Burton, 1994). This bias can be a result of large otoliths in slow growing fish confounding the relationship between length and otolith size and resulting in relatively small back-calculated length-at-age for younger ages (Campana, 1990). However, it can also result from selectivity bias in the sample whereby the faster younger fish are disproportionately selected for by the fishing gears (Lucena and O'Brien, 2001; Ballagh et al., 2006) or where size-selective mortality has removed fast growing individuals from older age classes, thereby biasing the population demographics (Fossen et al., 1999). Differences in the mean back-calculated lengths-at-age from all annuli and the last annulus can therefore be used to infer any biases such as selectivity on sampling (Vaughan and Burton, 1994). Analysis of variance (ANOVA) and Student's *t*-test were used to compare mean back-calculated length-at-age from all annuli to mean back-calculated length-at-age from the last annulus only.

Substitution of data

Back-calculated lengths-at-age from all annuli were compared to observed lengths-at-age by using ANOVA and *t*-tests. Comparisons were made to determine the ages for which there were no differences between back-calculated and observed length-at-age to test the hypothesis that supplementing back-calculated length-at-age with observed or adjusted length-at-age can provide estimates of growth parameters that are more appropriate representations of the population (Ballagh et al., 2006). Observed and adjusted length-at-age data were substituted with back-calculated length-at-age data (BC-all and BC-last) for the first few consecutive ages that were significantly different from observed length-at-age. This procedure resulted in several combinations of data from different methods for determining length-

at-age (back-calculated, observed, and adjusted), and is hereafter referred to as substitution.

VBGF curves were fitted to the substituted length-at-age data sets by using nonlinear regression. Likelihood ratio tests were performed to test for differences in growth among the different substituted combinations of length-at-age data. Where differences were found, multiple comparisons by using likelihood ratio tests with Bonferroni adjustments (Eq. 4) were performed on pairs of substituted data combinations.

Results

Growth

A high degree of variability was observed among the VBGF parameter estimates from the different methods for estimating length-at-age for both species and sexes (Table 2). The two back-calculation methods consistently yielded lower estimates of L_{∞} and higher estimates of K and t_0 than the observed and adjusted methods. Less error was also observed in the estimates of L_{∞} and t_0 for the back-calculated methods than for the observed and adjusted methods.

Comparison of the VBGF growth estimates by using overall likelihood ratio tests revealed significant differences in growth estimates among the methods for both species and sexes (*S. commerson* females: $\chi^2=678.9$, $df=12$, $P<0.0001$, males: $\chi^2=704.4$, $df=12$, $P<0.0001$; *S. semifasciatus* females: $\chi^2=849.4$, $df=12$, $P<0.0001$, males: $\chi^2=913.1$, $df=12$, $P<0.0001$). Multiple comparisons revealed some consistent patterns in growth estimates among methods (Table 3). Significant differences were observed between the back-calculation methods (BC-all, BC-last) and the adjusted and observed methods (Adj-cat, Adj-frm, Obsv), and no significant differences were found between the two back-calculation methods for both species. There were no significant differences between the two adjusted methods for both sexes of *S. commerson* and female *S. semifasciatus*, whereas the two adjusted methods differed significantly for male *S. semifasciatus*. No significant differences were found between the adjusted and observed methods for both species, with the exception of the formula adjusted and observed methods for female *S. commerson*.

Comparison of VBGF parameter estimates by using likelihood ratio tests revealed further differences ($P<0.05$, $df=1$) between the methods that differed in the overall likelihood ratio test comparisons. For *S. commerson*, all VBGF parameters differed significantly between individual methods with the exception of the formula adjusted and observed methods for females, for which none of the VBGF parameters differed significantly. For *S. semifasciatus*, significant differences were observed for all VBGF parameters in comparisons between the back-calculation methods and the adjusted and observed methods. No significant difference was observed between any of the VBGF parameter estimates for comparisons between observed and formula-

Table 2

Estimates for von Bertalanffy growth function parameters: growth coefficient (K), theoretical maximum length (L_{∞}), and theoretical age where length is equal to zero (t_0) (\pm standard error), sample numbers (n), age ranges, and adjusted R^2 values from different methods (observed [Obsv], category-adjusted [Adj-cat], formula adjusted [Adj-frm], back-calculation to all annuli [BC-all], and back-calculation to the last annulus only [BC-last]) for estimating length-at-age for *Scomberomorus commerson* and *S. semifasciatus*.

Species	Sex	Method	K	L_{∞} (mm)	t_0 (years)	n	Min age	Max age	R^2_{adj}
<i>S. commerson</i>	Female	Obsv	0.16 (0.03)	1508 (153)	-4.55 (1.02)	288	1	15	0.7592
		Adj-cat	0.11 (0.03)	1725 (173)	-5.56 (1.08)	247	1	11	0.7806
		Adj-frm	0.10 (0.03)	1735 (186)	-5.86 (1.18)	239	1	11.9	0.7821
		BC-all	0.51 (0.03)	1248 (13)	-0.39 (1.06)	811	1	10	0.8473
		BC-last	0.45 (0.05)	1273 (25)	-0.68 (0.15)	216	1	10	0.8603
	Males	Obsv	0.21 (0.06)	1186 (109)	-5.77 (2.64)	213	1	11	0.8396
		Adj-cat	0.20 (0.06)	1202 (55)	-5.25 (1.58)	187	0.5	11	0.5715
		Adj-frm	0.21 (0.06)	1186 (47)	-5.18 (1.52)	187	0.8	11	0.586
		BC-all	0.75 (0.05)	1047 (9)	-0.18 (0.07)	601	1	9	0.588
		BC-last	0.74 (0.09)	1063 (15)	-0.27 (0.15)	157	1	9	0.8168
<i>S. semifasciatus</i>	Female	Obsv	0.29 (0.06)	896 (22)	-4.08 (0.78)	306	0	9	0.555
		Adj-cat	0.23 (0.06)	938 (38)	-4.64 (1.13)	310	1	9	0.5371
		Adj-frm	0.20 (0.06)	929 (41)	-5.40 (1.44)	306	0.6	9	0.4937
		BC-all	1.04 (0.05)	827 (6)	0.19 (0.04)	923	1	9	0.8243
		BC-last	0.99 (0.07)	834 (8)	0.15 (0.07)	289	1	9	0.797
	Males	Obsv	0.31 (0.04)	840 (13)	-3.87 (0.43)	323	0	10	0.7049
		Adj-cat	0.34 (0.04)	845 (14)	-2.86 (0.43)	325	0.5	10	0.6822
		Adj-frm	0.28 (0.04)	847 (16)	-3.77 (0.54)	323	0.5	10.6	0.661
		BC-all	1.04 (0.05)	781 (5)	0.14 (0.04)	974	1	10	0.8262
		BC-lLast	0.98 (0.07)	785 (6)	0.08 (0.07)	300	1	10	0.8268

Table 3

Chi-squared values for the overall likelihood ratio test between growth estimates from different methods (category adjusted [Adj-cat], formula adjusted [Adj-frm], back-calculation to all annuli [BC-all], back-calculation to the last annulus only [BC-lLast], and observed [Obsv]) for estimating length-at-age for *Scomberomorus commerson* and *S. semifasciatus* (* indicates significant difference at $P < 0.005$, Bonferroni-adjusted α for multiple comparisons, $df=3$).

Species	Sex	Method	Adj-frm χ^2	BC-all χ^2	BC-lLast χ^2	Obsv χ^2
<i>S. commerson</i>	Female	Adj-cat	1.2	197.1*	114.9*	9.2
		Adj-frm		162.6*	101.0*	13.6*
		BC-all			10.4	464.9*
		BC-last				229.9*
	Male	Adj-cat	0.575	158.3*	80.8*	5.4
		Adj-frm		161.6*	86.0*	8.1
		BC-all			12.0	496.7*
		BC-last				240.6*
<i>S. semifasciatus</i>	Female	Adj-cat	7.7	172.9*	167.3*	16.3*
		Adj-frm		139.8*	147.7*	23.7*
		BC-all			0.546	524.8*
		BC-last				350.9*
	Male	Adj-cat	16.6*	169.2*	174.4*	55.8*
		Adj-frm		102.9*	136.8*	43.6*
		BC-all			0.37	561.7*
		BC-last				434.0*

adjusted methods for both sexes and the observed and category-adjusted methods for female *S. semifasciatus*. Significant differences in the estimates of K and t_0 were observed between the observed and category-adjusted methods, and no significant difference was observed between any of the VBGF parameters for the two adjusted methods for male *S. semifasciatus*.

Selectivity effects

Comparison of length-at-age between the two back-calculation methods using ANOVA revealed significant differences in mean length-at-age existed for female *S. commerson* only ($F_{1,7}=2.13$, $P=0.039$). Multiple t -tests revealed differences in mean back-calculated length for age-1 female ($t_{245}=3.94$, $P<0.001$), and age-1 ($t_{184}=2.68$, $P=0.008$), and age-2 ($t_{129}=2.38$, $P<0.019$) male *S. commerson*.

Substitution of data

Comparison of length-at-age between the back-calculation to all annuli and observed methods with ANOVA revealed significant differences in mean length-at-age for both species and sexes (*S. commerson* females: $F_{1,9}=32.3$, $P<0.001$, males: $F_{1,8}=37.8$, $P<0.001$; *S. semifasciatus* females: $F_{1,8}=52.5$, $P<0.001$, males: $F_{1,9}=53.9$, $P<0.001$). For *S. commerson*, t -tests revealed differences in mean length between back-calculated and observed methods for the first four consecutive ages for both sexes (females age 1: $t_{332}=20.39$, $P<0.001$, age 2: $t_{218}=5.44$, $P<0.001$, age 3: $t_{132}=2.14$, $P=0.034$, age 4: $t_{140}=3.54$, $P<0.001$; males age 1: $t_{242}=17.72$, $P<0.001$, age 2: $t_{172}=8.61$, $P<0.001$, age 3: $t_{104}=3.64$, $P<0.001$, age 4: $t_{103}=3.94$, $P<0.001$), as well as age 6 for males ($t_{47}=2.68$, $P=0.01$). For *S. semifasciatus*, differences in mean length between back-calculated and observed methods were observed for the first three consecutive ages for females (age 1: $t_{353}=16.61$, $P<0.001$, age 2: $t_{329}=6.00$, $P<0.001$, age 3: $t_{250}=3.37$, $P<0.001$), and the first two consecutive ages for males (age 1: $t_{332}=16.5$, $P<0.001$, age 2: $t_{332}=5.43$, $P<0.001$). Consequently, substitution of observed and adjusted length-at-age with back-calculated length-at-age was done for the first four ages for male and female *S. commerson*, the first three ages for female *S. semifasciatus*, and the first two ages for male *S. semifasciatus*. Von Bertalanffy growth functions were then fitted to the combined data sets (Table 4, Fig. 2).

Growth estimates from substitution displayed a general pattern of higher estimates of K and lower estimates of L_∞ than the respective observed or adjusted methods alone, and higher estimates of L_∞ than the respective back-calculated methods alone (Table 4). All observed length-at-age data beyond age 8 for *S. semifasciatus*, and male *S. commerson*, and age 9 for female *S. commerson*, had a greater length than the back-calculated and substituted VBGF estimates (Fig. 2). Comparison of the different combinations of substituted methods revealed no significant differences

for *S. semifasciatus* (Table 5). However, there were significant differences between some combinations for *S. commerson*, mostly for females (Table 5). Notably, all the significant differences occurred between combinations with BC-last and BC-all substituted data, with the combination of BC-last and observed data differing to all combinations with BC-all data for female *S. commerson*.

Discussion

Alternative methods for estimating length-at-age from otoliths resulted in significant differences in estimates of growth. A clear pattern emerged that revealed large differences between the back-calculation (BC-all, BC-last) methods and the observed and adjusted methods (Obsv, Adj-cat, Adj-frm) for both species of mackerel. However, the pattern was more pronounced for *S. commerson* than for *S. semifasciatus*, most likely because of the more pronounced effects of selectivity on *S. commerson* length-at-age data. The method of substituting length-at-age data obtained from observed or adjusted methods with back-calculated length-at-age produced different estimates of growth to the individual methods. This technique proved valuable for providing estimates of population growth, which are likely to be more accurate than those provided with the individual methods alone, particularly in the presence of selectivity biases; the technique also improved estimates of length for younger ages over observed or adjusted methods and provided more realistic estimates of mean maximum length than estimates from back-calculation methods alone.

A significant difference in growth between back-calculated length-at-age to all annuli and the last annulus was observed for *S. commerson* if the result of the overall likelihood ratio test is taken in isolation of the multiple comparisons with other methods (i.e., $P<0.05$), indicating that selectivity bias was inherent in *S. commerson* samples. Comparison of the two back-calculation methods for *S. commerson* indicated that fish are fully recruited to the fishery at approximately 900 mm fork length, above which no difference in length-at-age was observed between the back-calculation methods. No significant difference was observed between the two back-calculation methods for *S. semifasciatus* and therefore indicated that selectivity was not biasing length-at-age data.

In choosing which method(s) to use in determining length-at-age for growth estimation, careful consideration should be given to the growth characteristics of a species. We examined relatively fast growing species with similar growth characteristics in this study, and thus some of our conclusions may not be applicable or practical when applied to other species with different growth characteristics. Each method for determining length-at-age has its pros and cons, which differ depending on the growth characteristics of the species in consideration.

Table 4

Von Bertalanffy growth function parameter estimates (growth coefficient [K], theoretical maximum length [L_{∞}], and theoretical age where length is equal to zero [t_0], \pm standard error), sample numbers (n), age ranges, and adjusted R^2 values from different combinations of substituted methods (observed [Obsv], category adjusted [Adj-cat], formula adjusted [Adj-frm], back-calculation to all annuli [BC-all], and back-calculation to the last annulus only [BC-last]) for estimating length-at-age for *Scomberomorus commerson* and *S. semifasciatus*.

Species	Sex	BC data	Method	K	L_{∞} (mm)	t_0 (years)	n	Min age	Max age	R^2_{adj}
<i>S. commerson</i>	Female	BC-all	Obsv	0.41 (0.02)	1319 (17)	-0.60 (0.07)	741	1	15.0	0.84
		BC-all	Adj-cat	0.43 (0.02)	1304 (16)	-0.55 (0.07)	747	1	11.0	0.84
		BC-all	Adj-frm	0.44 (0.02)	1295 (15)	-0.53 (0.07)	750	1	11.9	0.84
		BC-last	Obsv	0.29 (0.03)	1411 (33)	-1.30 (0.19)	263	1	15.0	0.87
		BC-last	Adj-cat	0.31 (0.03)	1383 (29)	-1.18 (0.17)	268	1	11.0	0.87
		BC-last	Adj-frm	0.32 (0.03)	1366 (26)	-1.14 (0.17)	271	1	11.9	0.87
	Male	BC-all	Obsv	0.60 (0.04)	1092 (12)	-0.39 (0.08)	562	1	11.0	0.81
		BC-all	Adj-cat	0.63 (0.04)	1084 (12)	-0.35 (0.08)	561	1	11.0	0.81
		BC-all	Adj-frm	0.64 (0.04)	1081 (11)	-0.34 (0.07)	573	1	11.0	0.82
		BC-last	Obsv	0.54 (0.06)	1118 (15)	-0.62 (0.17)	191	1	11.0	0.84
		BC-Last	Adj-cat	0.58 (0.06)	1108 (14)	-0.55 (0.16)	190	1	11.0	0.84
		BC-Last	Adj-frm	0.57 (0.06)	1103 (13)	-0.57 (0.15)	202	1	11.0	0.84
<i>S. semifasciatus</i>	Female	BC-All	Obsv	1.02 (0.06)	830 (7)	0.18 (0.04)	828	1	9.0	0.81
		BC-All	Adj-cat	1.02 (0.05)	830 (7)	0.18 (0.04)	846	1	9.0	0.82
		BC-All	Adj-frm	1.08 (0.06)	821 (6)	0.21 (0.04)	894	1	9.0	0.82
		BC-Last	Obsv	0.95 (0.07)	841 (8)	0.12 (0.07)	295	1	9.0	0.80
		BC-Last	Adj-cat	0.95 (0.07)	840 (7)	0.12 (0.07)	312	1	9.0	0.80
		BC-Last	Adj-frm	1.02 (0.07)	828 (6)	0.17 (0.06)	359	1	9.0	0.79
	Male	BC-All	Obsv	1.03 (0.06)	790 (7)	0.14 (0.04)	748	1	10.0	0.80
		BC-All	Adj-cat	1.04 (0.06)	787 (7)	0.15 (0.04)	774	1	10.0	0.80
		BC-All	Adj-frm	1.13 (0.06)	771 (6)	0.18 (0.04)	825	1	10.6	0.79
		BC-Last	Obsv	0.96 (0.06)	794 (6)	0.08 (0.06)	306	1	10.0	0.83
		BC-Last	Adj-cat	0.96 (0.06)	791 (6)	0.07 (0.06)	332	1	10.0	0.83
		BC-Last	Adj-frm	1.00 (0.06)	776 (5)	0.07 (0.06)	383	1	10.6	0.78

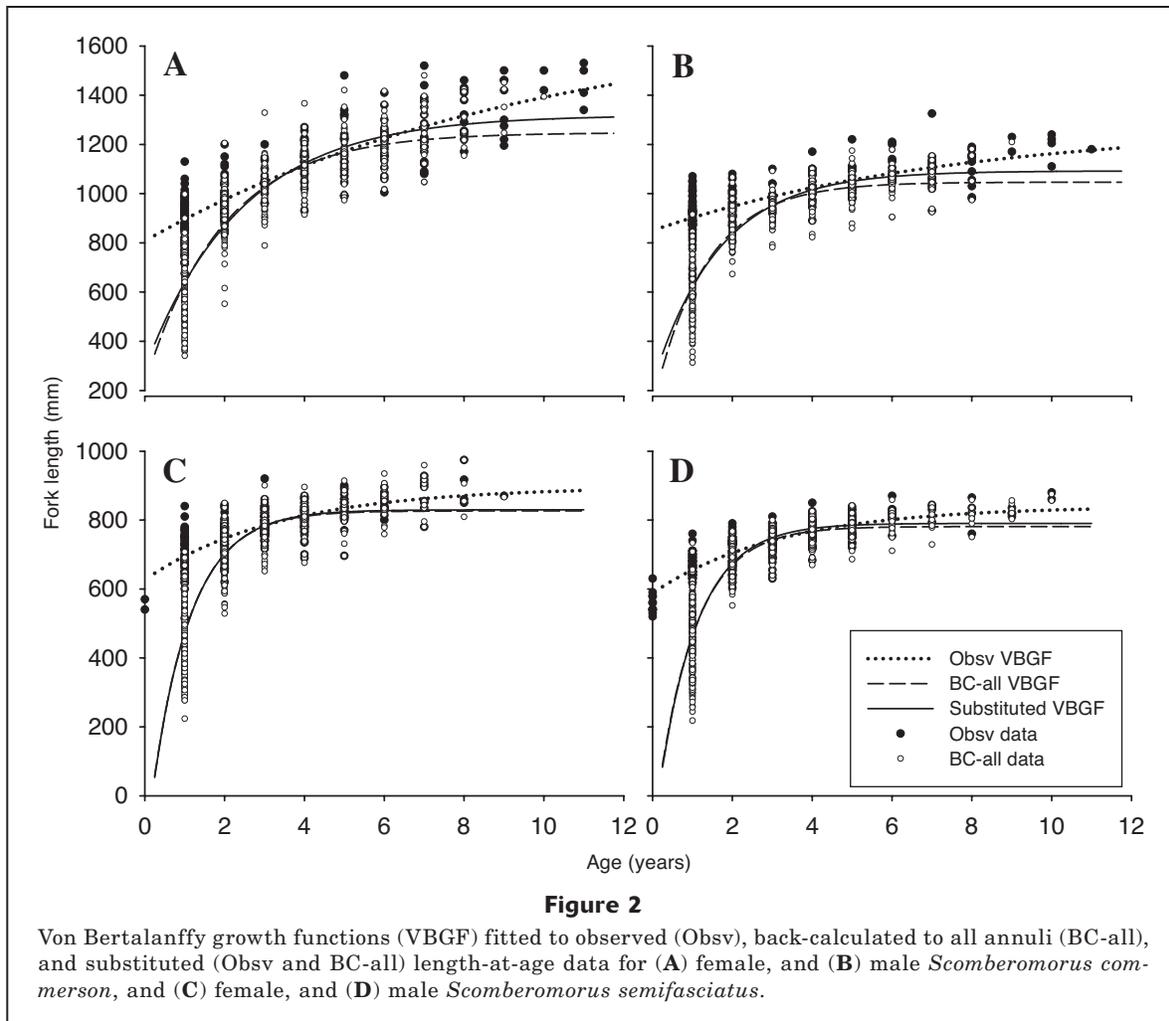
Observed length-at-age, although being relatively easy to obtain compared to other data, can have the most aging error given that any growth beyond a whole year is not accounted for. The magnitude and frequency of aging error has been shown to be uniform across all ages for *S. semifasciatus* (Marriott et al., 2010). However, given the rapid growth of such species in the first few years, aging error for younger ages will have more influence on growth estimates than aging error in older ages. Although this problem can be exacerbated for fast growing species such as *S. commerson* and *S. semifasciatus*, uniform aging error across age classes may be a lesser issue for growth estimation of long-lived, slow growing fish, and observed length-at-age could be more accurate if samples are collected after the period of annuli formation and the opaque increment at the edge is included in age estimates.

Adjustment methods for determining length-at-age theoretically provide a more accurate estimate of age than observed length-at-age by accounting for growth on a finer temporal scale, especially if the spawning period and period of annuli formation is discrete (e.g., DeVries and Grimes, 1997). The formula-adjustment

method, however, is useful only if population-specific spawning and annuli formation periods are known for a given species, and it is less useful if the species has a protracted spawning period or if the timing of annuli formation varies (e.g., Williams et al., 2005). The category-adjustment method is useful for assigning ages to cohorts for use in assessment models (Begg et al.⁴) as well as for estimating growth (Shepard et al., 2010).

Back-calculation is useful for estimating selectivity effects (Campana, 1990; Lucena and O'Brien, 2001; Ballagh et al., 2006), providing length-at-age estimates for younger fish that may not be seen in fishery-dependent samples (Campana, 2001; Lopez-Abellan et al., 2008), providing comparisons between different populations (Johnson et al., 1983; Fable et al., 1987; Ballagh et al., 2006), and assessing individual growth variability (Fossen et al., 1999; Pilling et al., 2002).

⁴ Begg, G. A., C. C.-M. Chen, M. F. O'Neill, and D. B. Rose. 2006. Stock assessment of the Torres Strait Spanish mackerel fishery. CRC Reef Research Centre Technical Report No 66, 81 p. CRC Reef Research Centre, Townsville, Australia.



However, this method can be influenced by statistical dependency whereby estimated lengths at younger ages are dependent on lengths from older ages through the back-calculation process and are therefore susceptible to bias in the presence of size-selective mortality (Vaughan and Burton, 1994; Pilling et al., 2002). Other drawbacks of back-calculation include the specialized equipment and software needed and the significant time required to obtain data.

We demonstrated that although back-calculation was effective for estimating length-at-age for younger ages in the presence of selectivity within a fishery that selects for the faster growing younger fish, it appears to underestimate mean maximum length (L_{∞}). This finding is shown by observed length-at-age data being consistently higher than the back-calculated VBGF for older age classes and is subject to the assumption that there is little or no selectivity acting on older fish. The underestimation of back-calculated mean maximum length is likely due to three effects: smaller length-at-age for younger fish; weighting of data in younger ages; and the negative correlation between the VBGF parameters of L_{∞} and K . Back-calculating to all annuli

results in a disproportionate amount of data for young ages which, depending on the growth estimation method used, gives more weight to younger ages when fitting a VBGF. Because the VBGF parameters L_{∞} and K have been shown to be negatively correlated (Pilling et al., 2002), increasing the estimate of K through smaller length-at-age for younger ages, or a weighting of data in younger ages, will inevitably reduce the estimate of L_{∞} , and thus underestimate average maximum length. One option for overcoming this problem could be to constrain L_{∞} to the largest observed length, although some prior knowledge of the size-selectivity pattern of sampling gears is required to make an informed decision to constrain parameters (Gwinn et al., 2010),

Fishery-independent sampling can improve estimates of growth through the collection of small, slower growing young fish not fully represented in fishery-dependent samples. However, fishery-independent sampling is typically expensive and not always possible or practical. Methods have been developed to correct bias in length-at-age data; however, these require previous knowledge of selectivity patterns, mark-recapture data or intensive sampling over several consecutive

Table 5

Chi-squared values for overall likelihood ratio tests between growth estimates from different combinations of substituted methods (observed [Obsv], category adjusted [Adj-cat], formula adjusted [Adj-frm], back-calculation to all annuli [BC-all], and back-calculation to the last annulus only [BC-last]) of estimating length-at-age for *Scomberomorus commerson* and *S. semifasciatus* (* indicates significant difference at $P < 0.0033$, α was Bonfferoni adjusted for multiple comparisons, $df=3$).

Species	Sex	Methods	BC-all- Adj-cat χ^2	BC-all- Adj-frm χ^2	BC-last- Obsv χ^2	BC-last- Adj-cat χ^2	BC-last- Adj-frm χ^2
<i>S. commerson</i>	Female	BC-all-Obsv	0.087	0.434	13.8*	13.0	12.6
		BC-all-Adj-cat		0.138	15.3*	14.4*	13.7
		BC-all-Adj-frm			16.5 *	15.4*	14.3*
		BC-last-Obsv				0.073	0.680
		BC-last-Adj-cat					0.349
	Male	BC-all-Obsv	0.193	0.428	11.2	10.4	9.6
		BC-all-Adj-cat		0.050	12.7	11.6	10.5
		BC-all-Adj-frm			14.0*	12.6	11.3
		BC-last-Obsv				0.203	0.719
		BC-last-Adj-cat					0.220
<i>S. semifasciatus</i>	Female	BC-all-Obsv	0.001	0.709	0.957	0.853	0.103
		BC-all-Adj-cat		0.802	0.992	0.879	0.110
		BC-all-Adj-frm			3.6	3.5	0.538
		BC-last-Obsv				0.020	1.8
		BC-last-Adj-cat					1.6
	Male	BC-all-Obsv	0.199	5.5	0.529	1.346	8.8
		BC-all-Adj-cat		3.9	0.581	0.934	6.7
		BC-all-Adj-frm			6.2	4.9	1.9
		BC-last-Obsv				0.374	9.0
		BC-last-Adj-cat					6.3

years (Gwinn et al., 2010). Recently, several different methods for reducing bias in growth estimates from length-at-age data from size-selective samples have been proposed, including multinomial estimation models (Taylor et al., 2005), multigrowth model inference (Thorson and Simpfendorfer, 2009) and biologically based von Bertalanffy fitting procedures (Gwinn et al., 2010).

Substitution was shown to be a potentially useful method for providing more accurate estimates of population growth than the individual methods alone in the presence of selectivity pressure for faster growing young fish. Given that a significant difference in growth was observed between data substituted with the two different back-calculation methods for *S. commerson*, it is presumed that back-calculating data to all annuli would be the most appropriate back-calculation method to use in substitution in this instance given the selectivity bias observed in the young age classes. We therefore recommend that back-calculated length-at-age data from all annuli for young age classes be combined with observed or adjusted length-at-age data from older age classes to estimate population growth in the presence of selectivity favoring faster growing younger fish. Further studies should be undertaken to investigate the appropriateness of different methods for length-at-age

determination and the effectiveness of substitution for species with different growth characteristics and under different selectivity regimes of fisheries.

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