Seasonal growth of King George whiting (*Sillaginodes punctata*) estimated from length-at-age samples of the legal-size harvest

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Abstract—Samples of 11,000 King George whiting (*Sillaginodes punctata*) from the South Australian commercial and recreational catch, supplemented by research samples, were aged from otoliths. Samples were analyzed from three coastal regions and by sex. Most sampling was undertaken at fish processing plants, from which only fish longer than the legal minimum length were obtained. A left-truncated normal distribution of lengths at monthly age was therefore employed as model likelihood. Mean length-at-monthly-age was described by a generalized von Bertalanffy formula with sinusoidal seasonality. Likelihood standard deviation was modeled to vary allometrically with mean length. A range of related formulas (with 6 to 8 parameters) for seasonal mean length at age were compared. In addition to likelihood ratio tests of relative fit, model selection criteria were a minimum occurrence of high uncertainties (>20% SE), of high correlations (>0.9, >0.95, and >0.99) and of parameter estimates at their biological limits, and we sought a model with a minimum number of parameters. A generalized von Bertalanffy formula with t_0 fixed at 0 was chosen. The truncated likelihood alleviated the overestimation bias of mean length at age that would otherwise accrue from catch samples being restricted to legal sizes.

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In this study, we estimated growth curves from six data sets of fish sampled from the commercial and recreational catch of an important fish species in South Australia (Fig. 1), King George whiting (*Sillaginodes punctata*). Like many temperate fish populations, recruitment and growth can be assumed to follow a yearly cycle. A variety of methods have been used to measure seasonal variation in fish growth including mark-recapture (Francis, 1988; Coggan, 1997) and otolith annulus-diameter increments in combination with tetracycline marking (Panfili et al., 1994; Fabré and St. Paul, 1998; Francis et al., 1999). The method used in our study is the most widely employed, of fitting to lengths-at-age, where the age of each sampled fish is read as a count of yearly otolith annuli from samples of the harvest.

The model-fitting algorithm had three key objectives, each to represent a specific feature of the growth of South Australian King George whiting, or of the data set. These were expressed mathematically as deviations from a standard 3-parameter von Bertalanffy model fitted with a normal likelihood.

The first two objectives were elaborations on the standard von Bertalanffy growth curve (understood as a deterministic function of mean length versus age). The first objective was to make seasonality explicit in the growth curve (Pitcher and MacDonald, 1973; Somers, 1988; Hoenig and Hanumara, 1990; Pauly and Gaschütz[1]) and the second objective was to allow a wider range of curvatures by using the *r*-exponent (Schnute, 1981).

For application of this growth description in length- and age-based stock assessment modeling, we also estimated the shape of the length-at-age probability density function (pdf), which quantifies the distribution of fish of different lengths at each age.

The principal regulation of both recreational and commercial King George whiting harvest is by legal minimum length (LML); fish smaller than the LML cannot be landed and must be returned to the sea. Therefore fish obtained from the catch are a biased sample. The third objective was to explicitly account for the absence of fish below the LML, for which a truncated pdf was used. This truncated normal density, the pdf of observed lengths-at-age, was also used as the likelihood for each individual sample.

A range of models were examined that met these three objectives. These included a seasonal version of the Richards (1959) model proposed by Akamine (1993), which makes different use of the *r*-exponent. Therefore a fourth objective was to apply standard statistical model selection techniques. Methods to choose the most appropriate model for a given growth data set were reviewed by Quinn and Deriso (1999). Hierarchical model fits are statistically comparable using their likeli-

[1] Pauly, D., and G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. Demersal Fish Committee, ICES council meeting 1979/G:24. ICES, Palægade 2-4 DK-1261 Copenhagen K, Denmark.

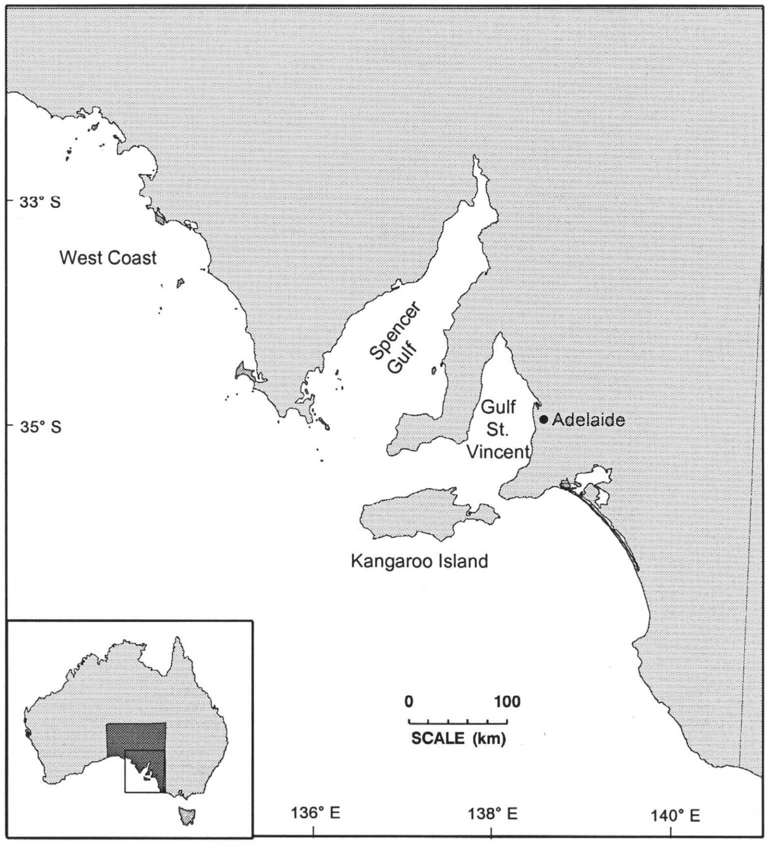

Figure 1

South Australian coastal waters. King George whiting (*Sillaginodes punctata*) are found predominantly in the two Gulfs, and along the West Coast.

hood ratio (Kimura, 1980; Rice, 1995). We sought to reduce the original 8-parameter model and employed likelihood ratio tests to evaluate the relative fit of the simpler models tested. We specify and apply a set of selection criteria below, seeking one common model form for six data sets to describe the length-at-age distributions. A 7-parameter generalized seasonal von Bertalanffy model, with t_0 fixed at zero, was chosen.

In addition, we applied an allometric relationship (a power curve) to fit weight versus length for this population.

That the samples are not uniform by length in commercial catch is common to most fisheries. The absence of fish below LML or below the lengths selected by the fishing gear, inevitable when sampling is from the landed catch, creates an overestimation bias of mean length-at-age, because faster growing fish reach the legal stock sooner and are thus over-represented in those samples. This sampling bias was taken into consideration by the use of a truncated model likelihood assuming zero probability of capture below legal size. In practice, the clear advantage of samples from the landed (commercial or recreational) harvest is a substantially lower cost than the alternative of fishery-independent samples gathered, usually by researchers, at sea.

The specific length-dependent bias in sampling changed during the time of the study. The LML was raised from 280 mm to 300 mm. Also, some of the samples were gathered by researchers who landed all, notably smaller fish. By applying one of three different likelihoods to any given sample, having different truncation lengths of 280 mm, 300 mm, or no truncation, all fish samples were combined in a single length-at-age estimation for each of three regional subpopulations, and by sex.

Materials and methods

A total of 11,164 King George whiting were sampled between 1995 and 1998 from across the main fishery area of South Australia. Most samples were obtained by subsampling the commercial catch at local fish processing plants or by purchasing fish from commercial processors. Some samples were provided as frozen fish frames (fillets removed) by recreational fishermen, and the remainder were caught on scientific cruises. Each fish was measured for total (TL) and standard lengths (SL) to the nearest mm, and weighed to 0.1 g. Gonads were removed, sexed, and weighed. The sagittae, the largest pair of otoliths, were removed from each fish for age determination.

Samples were subdivided into six data sets: three spatial regions and by sex (Table 1). Movement studies based

Table 1

Summary of data sets, each fish measured for age, length, and weight in the King George whiting analysis. Samples from commercial and recreational fisheries were regulated by a 280-mm legal minimum length (LML) before 1 September 1995, a 300-mm minimum length thereafter.

					Sample size		
Area	Area abbreviation	Sex	Beginning date	End date	Researchers	Fisheries 280 LML	Fisheries 300 LML
Gulf St. Vincent and nortern Kangaroo Island	GSV	male	4 Aug 94	17 Feb 99	293	503	1139
		female	4 Aug 94	17 Feb 99	373	615	1343
Spencer Gulf	SG	male	23 Apr 94	30 Sep 97	267	298	924
		female	23 Apr 94	30 Sep 97	363	441	1300
South Australian West Coast	WC	male	27 Apr 94	18 May 97	167	805	608
		female	27 Apr 94	19 May 97	226	857	642

on tag recoveries over three decades (Fowler and March[2]) indicated three largely self-sustaining subpopulations: Gulf St. Vincent, Spencer Gulf, and West Coast (Fig. 1).

Young fish (two- and three-year-olds) were aged by interpretation of the macrostructure of the whole sagittae. For fish with more complex otoliths, the otolith was snapped in two across the posterior-anterior axis through the center, exposing the transverse face of both halves. One of these halves was burnt in a bunsen flame and then examined with a binocular dissecting microscope at 6–20× magnification. The surface being examined was smeared with immersion oil. The alternating opaque and translucent zones were counted. The periodicity of formation of this macrostructure in sagittae of King George whiting has been validated and the following algorithm was developed for conversion of ring count to age (Fowler and Short, 1998):

$$a = 12N + m_b + m_c,$$

where a = age in months;
N = number of opaque zones;
m_b = 8 = number of months from universal birth date (i.e. 1 May) midway through spawning season to the end of the year; and
m_c = number of months from the start of year to the month of capture.

Some samples of fish were scaled in the commercial processing plant prior to weighing and measuring for length. Although this process did not affect their lengths, it did result in an appreciable loss of weight. Consequently, for estimation of weight-length relationships we corrected the weights of scaled fish using a linear relationship that was derived by weighing 155 fish before and after scaling. This linear relationship was

$$\textit{(corrected weight)} = 1.0176 \times \textit{(scaled weight)} + 3.5835 \ (r^2{=}0.99, P{<}0.001, \text{df}{=}154).$$

Growth: length-at-age

In order to make explicit the absence of fish samples smaller than LML, a truncated normal probability density function of length was used to describe the probability of capture of individual fish in each monthly age. This pdf was employed as the likelihood of observation of each individual, given its age. Truncation implies a zero predicted probability of observing a commercially or recreationally sampled fish less than LML. A few sublegal fish were measured and, being unrepresentative, were removed from the six data sets.

During the period of sampling, in September 1995, the regulated size of LML for commercial and recreational fishery samples was increased from 280 to 300 mm. The likelihood truncation length was thus a function of date of capture. This necessitated two forms of likelihood, for LMLs of 280 and 300 mm. Smaller numbers of samples obtained on scientific cruises were not subject to LML size controls. Thus a third, regular untruncated, likelihood was used to model research samples.

A normal likelihood was fitted to model the distribution of lengths at each age:

$$L = \frac{1}{\sqrt{2\pi}\,\sigma(a_i)} \exp\left[-\frac{1}{2}\left\{\frac{l_i - \bar{l}(a_i)}{\sigma(a_i)}\right\}^2\right], \qquad (1)$$

where l_i = length of fish sample i; and
a_i = age of fish sample i obtained from count of its otolith annuli.

[2] Fowler, A. J., and W. A. March. 2000. Adult movement patterns. *In* Development of an integrated fisheries management model for King George whiting (*Sillaginodes punctata*) in South Australia (A. J. Fowler and R. McGarvey, eds.), p. 83–104. FRDC Final Project Report 95/008. Fisheries Research and Development Corporation, PO Box 222, Deakin West ACT 2600, Australia.

The mean length-at-age

$$\bar{l}(a_i) = L_\infty \left\{ 1 - \exp\left[-K \left\langle \frac{a_i - t_0}{12} + \frac{u}{2\pi} \begin{Bmatrix} \sin\left(2\pi(a_i - \omega)/12\right) - \\ \sin\left(2\pi(t_0 - \omega)/12\right) \end{Bmatrix} \right\rangle \right] \right\}^r. \quad (2)$$

was modeled by a seasonally periodic von Bertalanffy growth formula, generalized by the inclusion of an exponent, r. Age (a_i) was in integral units of months, with May, the assumed date of birth at mean time of spawning of South Australian King George whiting, being month 1. Division by 12 in the mean length formula preserves the usual units of K where age is in years.

The seasonality function is sinusoidal, although more complex seasonality functions can be postulated that allow asymmetry in growth through the year. Values of the seasonality amplitude parameter $u > 1$ imply decreasing length in the yearly time of minimum growth (Pauly and Gaschütz[1]). We therefore constrained $u \le 1$, assuming that no shrinking in length occurs. With sine, the phase parameter (ω) gives the month of maximum growth, where months of age 1, 13, 25, etc. denote the birth month, May.

The likelihood standard deviation (σ) was modeled as an allometric function of mean length:

$$\sigma(a_i) = s_0 \cdot \left(\bar{l}(a_i)\right)^{s_1}. \quad (3)$$

This power function for standard deviation in terms of mean length, applied by Francis (1988) to fitting tag-recovery length increments, has the desired property that once growth stops, the standard deviation in lengths-at-age also ceases to change. Similarly, in winter months of slowed (or zero) mean length increase, change in standard deviation slows correspondingly.

The left-truncated normal likelihood, which applies to samples from commercial and recreational fishermen,

$$L_i = \begin{cases} \dfrac{1}{\sigma(a_i)} \exp\left[-\dfrac{1}{2} \left\{ \dfrac{l_i - \bar{l}(a_i)}{\sigma(a_i)} \right\}^2 \right] \Bigg/ \\ \left\{ \displaystyle\int_{LML_i}^{+\infty} \dfrac{1}{\sigma(a_i)} \exp\left[-\dfrac{1}{2} \left\{ \dfrac{l - \bar{l}(a_i)}{\sigma(a_i)} \right\}^2 \right] dl \right\}, \text{ if } l_i \ge LML_i \\ 0, \text{ if } l_i < LML_i \end{cases} \quad (4)$$

postulates a probability cut-off to zero for landed samples less than LML and a normal probability, integrating to 1, for the range of legal lengths. LML is subscripted by the fish sample data point (i) to indicate that LML is either 280 or 300 mm depending on the date of capture of the fish. For research samples, for which all lengths could be observed, the full untruncated normal likelihood (Eq. 1) was used.

Parameters were estimated by minimizing the negative sum of log-likelihoods with the AD Model Builder estimation software (Otter Research Ltd., Sidney, B.C., Canada):

$$O = -\sum_{i=1}^{n} \ln(L_i). \quad (5)$$

Initial parameter values for all models tested were $t_0 = 0$, $u = 1$, $\omega = 9$, $s_0 = 0.1$, $s_1 = 1$, $r = 1$, with $L_\infty = 480$, $K = 0.36$ for females, and $L_\infty = 420$, $K = 0.6$ for males.

Confidence bounds on parameters for each data set were derived by assuming the standard asymptotic normal approximation. These were numerically calculated by AD Model Builder routines as the diagonal elements of the covariance matrix, the negative inverse of the Hessian matrix at the likelihood maximum.

Growth model choice

The full, seasonal, generalized von Bertalanffy model described above has eight parameters. A best-fitting model with the minimum number of parameters was sought. In cases where a model is overparameterized, high correlations between parameters appear and the confidence bounds widen. To test for a diagnosis of overparameterization and then to correct it by fixing otherwise freely estimated parameters, we applied the following algorithm based on standard methods of model selection:

1. Search for parameters that frequently show high correlations with other parameters, have high variances, or in estimation hit preset upper and lower bounds, beyond which biologically unrealistic values are being inferred.
2. Set those parameters to fixed likely values. This assumes a biologically likely value can be postulated. If not, use a mean value among the range of estimates obtained when the parameter is allowed to vary freely. A parameter may also be selected if it varies little among the range of data sets for which estimates are obtained.
3. Test for the change in negative log-likelihood to determine whether the reduced model is significantly less well fitting by using chi-square likelihood ratios.
4. Check that confidence intervals and correlations are reduced.

In addition, we seek model that converges reliably for all data sets. Satisfactory convergence should not depend on the initial parameter values chosen, but in some cases a new set of initial values can be tried for any given nonconverging data set. Convergence can also depend on the minimization algorithm or subroutine employed. However, for purposes of model selection, failure to converge for some data sets analyzed is an indication that the likelihood surface for that model is less smooth and the true global maximum may not always be obtained. Reliable convergence is particularly desirable when 1) bootstrapping, where nonconvergence leaves resampled data sets unestimated, and 2) for integration of growth into overall fishery stock assessment estimators, where finding more appropriate initial values for the growth parameters may be nontrivial, and the cause of nonconvergence of the overall estimation may not be easily traced to the growth submodel.

In addition to reduced versions of the model presented above, we fitted a related model proposed by Akamine (1993), which incorporates into the Richards (1959) growth curve a sinusoidal seasonality function like that of Equation 2.

Weight-at-length

Mean (corrected) weight versus total length was modeled by an allometric relationship:

$$\overline{w}(l_i) = \alpha\, l_i^{\beta} \tag{6}$$

A normal likelihood was again used. The standard deviation of the likelihood (i.e. of the fitted spread of observed weights about the mean given in Eq. 6) was assumed to vary linearly with length:

$$\sigma_w(l_i) = \sigma_{w0} + \sigma_{w1} l_i, \tag{7}$$

Parameter confidence bounds were estimated by a bootstrap of 1000 runs.

Results

Growth model choice

The generalized von Bertalanffy model (Eq. 2, abbreviated as gVB) gave the best fit with five of six data sets (Table 2). However for both gVB and the other 8-parameter model, Akamine-Richards (AR), correlations among parameters were unacceptably frequent and high (Table 2). Other evidence of overparameterization included frequent occurrence of wide confidence bounds (SE >20%, Table 2). High correlations and parameter uncertainties were most widespread for s_0 and s_1. The exponent, r, and seasonality amplitude, u, also occurred frequently with high uncertainty, and t_0 and r often were found in high correlations; t_0 hit both upper (7.99) and lower (–30) confidence bounds for some models with west coast data sets. As with standard von Bertalanffy models, t_0 quantifies the age (here, in months) at which length extrapolates to 0. The occurrence of u estimates hitting their upper bound of 1 is not due to model overparameterization but reflects the biological modeling decision to exclude shrinking.

The Akamine-Richards (AR) model varied widely among data sets in its relative closeness of fit, failed to converge for West Coast females, and did not yield a positive definite hessian for Gulf St. Vincent females. It was less well fitting than the gVB for all but one data set. The gVB model was therefore chosen as the better 8-parameter model, and subsequent reduced models were based on it in preference to AR.

From indicators summarized above, four parameters for defining overall mean length K, L_∞, t_0 and r, appear to be too many. Two obvious candidates for fixing to constant values were t_0 and r. These occurred frequently in indicators of model overparameterization. Both have intuitive biological default values at which they can be fixed, 0 and 1 respectively. Thus two 7-parameter models were run, with t_0 and r fixed, the latter (with r=1) reducing to a seasonal von Bertalanffy curve (Somers, 1988; Hoenig and Hanumara, 1990).

The fit with t_0 = 0 fixed was not significantly different from the full 8-parameter gVB for three of six data sets. This fit was tested by chi-square likelihood ratios at 95% confidence, indicated (Table 2) by successive likelihood-ratios of 1.92 or less, for comparing fits of hierarchical models differing by one in number of freely estimated parameters (Rice, 1995). The regular seasonal von Bertalanffy model (r=1, abbreviated as "reg VB") fitted less closely than gVB with t_0 = 0 for all six data sets; significantly worse for all Spencer Gulf and West Coast data sets. In addition, not shown in Table 2, the estimates of t_0 were frequently far from the realistic biological range near 0, often estimated at 10 to 20 months above or below. The frequency and magnitude of high correlations were substantially reduced with both 7-parameter models. Thus we choose to fix t_0 = 0 and let r freely vary.

The occurrence of very high correlation between s_0 and s_1 for all data sets and models (Table 2) suggested fixing one of them, in particular, the exponent, s_1. We set s_1 = 0.3 which fell near the average among the range of estimated values. The outcome was that t_0 (now free) hit its bound in three of six cases, thus exacerbating that pathology. When both t_0 = 0 and s_1 = 0.3 were fixed, the fits were uniformly poor (Table 2). Thus, the high correlation between the two allometric standard deviation parameters met with no obvious solution. However, these posed no wider problem because these parameters did not interact with those describing the mean length at age and the correlation between pairs of allometric parameters (such as α and β in the weight-length model, Eq. 6) is common and often unavoidable. Because a significantly better fit for the length-at-age standard deviation is sought, we let both s_0 and s_1 vary freely.

The gVB with t_0 = 0 fixed provided an optimal trade-off in reduced overparameterization and good fit: it achieved the objective of substantially reduced interparameter correlations without significantly worse fits in three of six cases. The remaining three data sets (Spencer Gulf females and males, West Coast females) had yielded unrealistic estimates of t_0 in full model gVB (of –17.9, –21.7, and the upper bound of 7.99 respectively). This model was therefore chosen and results from it presented below.

Growth: length-at-age

Estimated length at age showed seasonal periodic trends for the three regions and two sexes (Figs. 2–4). Estimates of u (seasonality amplitude) were constrained at the maximum allowed value of $u = 1$ for three of six data sets (Table 3). The peak month of maximum growth occurred in mid-

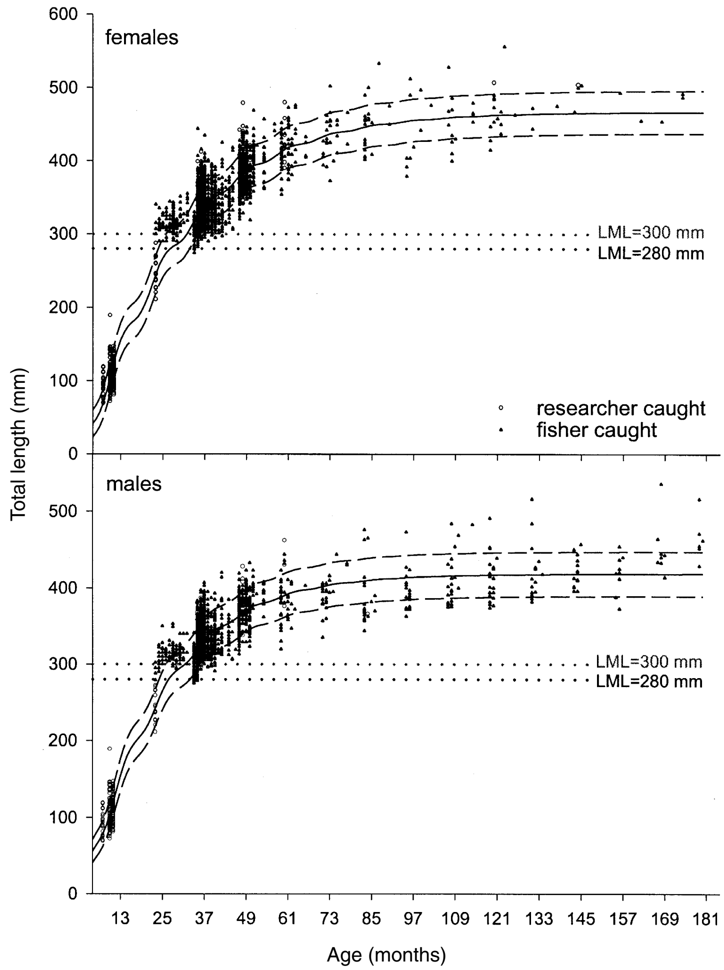

Figure 2

Lengths at age, beginning at 10 months, for Gulf St. Vincent King George whiting of both sexes. The solid line is the generalized seasonal von Bertalanffy mean length curve (Eq. 2) with $t_0 = 0$ fixed. Dashed lines indicate confidence bounds as normal likelihood standard deviation (Eq. 3). Dots represent individual observations of length-at-age.

summer (December–February) for all data sets except Gulf St. Vincent males.

Estimated (likelihood maximum) and observed distributions of lengths-at-age were plotted for Gulf St. Vincent females (Fig. 5) and males (Fig. 6). Because the estimation likelihood was fitted to formulas for mean (Eq. 2) and standard deviation (Eq. 3) of all ages at once, close fit to the majority of individual length-at-age distributions indicated a growth description mutually consistent among ages and a satisfactory approximation to monthly lengths at age overall.

For younger ages (28–35 months), the sampled frequencies were modeled by the truncated right-hand component of the normal pdf. The LML truncation lengths for each normal curve (280 or 300 mm in Figs. 5 and 6) indicated the lower limit of samples from the fishery. These samples are generally well fitted (Figs. 5 and 6), suggesting these truncated younger samples do contribute to the overall growth fit and that the truncated likelihood is effective in describing the monthly growth of the length-at-age cohort across LML into legal sizes. One exception yielding a less close fit were female fish aged 28 months taken under a LML of 280 mm (Fig. 5).

Weight-at-length

Parameter estimates for α and β (Eq. 6) covaried strongly. When all four parameters were allowed to freely vary, β differed little from 3.2 for all data sets (Table 4). Likelihood-ratio tests were therefore carried out to determine whether the model allowing β to vary freely yielded significantly better fits than one with three parameters and β fixed at 3.2. For all but Spencer Gulf males, likelihood-

Table 2

Criteria for model selection. gVB = generalized von Bertalanffy (Eq. 2); AR = Akamine-Richards (Akamine, 1993). Reduced gVB models fixed t_0 at 0 and s_1 at 0.3. Models in each data set are given in order of best to worst fitting. Differences in –logL provide likelihood ratio (L-ratio) test comparisons of the goodness of fit of successively reduced hierarchical models. An L-ratio of 1.92 (3.0) or greater implies a significantly better fit at 95% under a chi-square likelihood ratio test by comparison with reduced models of one (two) fewer parameters. High correlations between pairs of parameters are shown for three arbitrary categories: ** = >0.99; * = 0.95–0.99; pairs in this column unmarked by an asterisk had correlations of 0.9–0.95.

Data set	Model	No. of parameters	–logL	Successive L-ratios	Parameter pairs with |cors|>0.9	Parameters with SE/ estimate > 0.2	Parameters hitting estimation bound
Gulf St. Vincent females	gVB	8	10566.63		t_0~r**; t_0~K; r~K; s_1~s_0**	u, r, s_0, s_1	
	gVB t_0=0	7	10568.09	1.45	r~K; s_1~ s_0**	u, s_0, s_1	
	gVB t_0=0 & s_1=0.3	6	10570.38	2.29	r~K	u	
	reg VB	7	10571.27	0.89	L_∞~K; s_1~ s_0**	u, s_0, s_1	
	AR	8	10575.67	4.39	Hessian not positive definite	—	
Gulf St. Vincent males	gVB	8	8632.695		t_0~r**; t_0~K*; ω~K; s_1~ s_0**; t_0~ω*;r~K*; r~ω	u, r, s_0	
	AR	8	8632.695	0.00	t_0~r**; t_0~K*; r~K; s_1~ s_0**; t_0~ω*;ω~K;r~ω	u, r, s_0	
	gVB t_0=0	7	8632.759	0.06	r~K; s_1~ s_0**	u, s_0	
	reg VB	7	8632.908	0.15	t_0~u; s_1~ s_0**	u, s_0	
	gVB t_0=0 & s_1=0.3	6	8637.379	4.47	Hessian not positive definite	u	
Spencer Gulf females	gVB	8	9374.685		t_0~K; r~K; r~ t_0**; s_1~ s_0**	s_0, s_1	u=1
	gVB t_0=0	7	9391.099	16.41	K~ L_∞ r~K; s_1~ s_0**	s_0, s_1	u=1
	gVB t_0=0 & s_1=0.3	6	9392.176	1.08	K~ L_∞; r~K		
	AR	8	9420.834	28.66	K~ L_∞; s_1~ s_0**	s_0, s_1	u=1
	reg VB	7	9429.822	8.99	K~ L_∞; s_1~ s_0**	s_0, s_1	u=1
Spencer Gulf males	gVB	8	6620.955		t_0~r; s_1~ s_0**	r, s_0, s_1	u=1
	gVB t_0=0	7	6661.097	40.14	r~K; s_1~ s_0**	s_0, s_1	u=1
	AR	8	6728.644	67.55	K~ L_∞; s_1~ s_0**	s_0, s_1	u=1
	reg VB	7	6729.238	0.59	s_1~ s_0**	s_0, s_1	u=1
	gVB t_0=0 & s_1=0.3	6	7230.275	501.04	r~K	u	
West Coast females	AR	8	7771.561		K~ L_∞; r~ L_∞**; r~K*; s_1~ s_0**	s_0, s_1	t_0=-30
	gVB	8	7798.542	26.98	K~ L_∞; r~K; s_1~ s_0**	s_0, s_1	u=1
	gVB t_0=0	7	7805.209	6.67	K~ L_∞; r~K; s_1~ s_0**	s_0, s_1	u=1
	reg VB	7	7819.477	14.27	K~ L_∞*; s_1~ s_0**	s_0, s_1	u=1, t_0=7.99
	gVB t_0=0 & s_1=0.3	6	7828.671	9.19	K~ L_∞; r~K*	u	
West Coast males	gVB	8	7011.73		r~K*; s_1~ s_0**	u, s_0, s_1	t_0=7.99
	gVB t_0=0	7	7013.403	1.67	r~K*; r~u; s_1~ s_0**	u, r, s_0, s_1	
	reg VB	7	7083.513	70.11	K~ L_∞*; s_1~ s_0**		t_0=7.99
	gVB t_0=0 & s_1=0.3	6	7828.671	745.16	r~K*; r~u	u, r	
	AR	8	failed to converge	—			

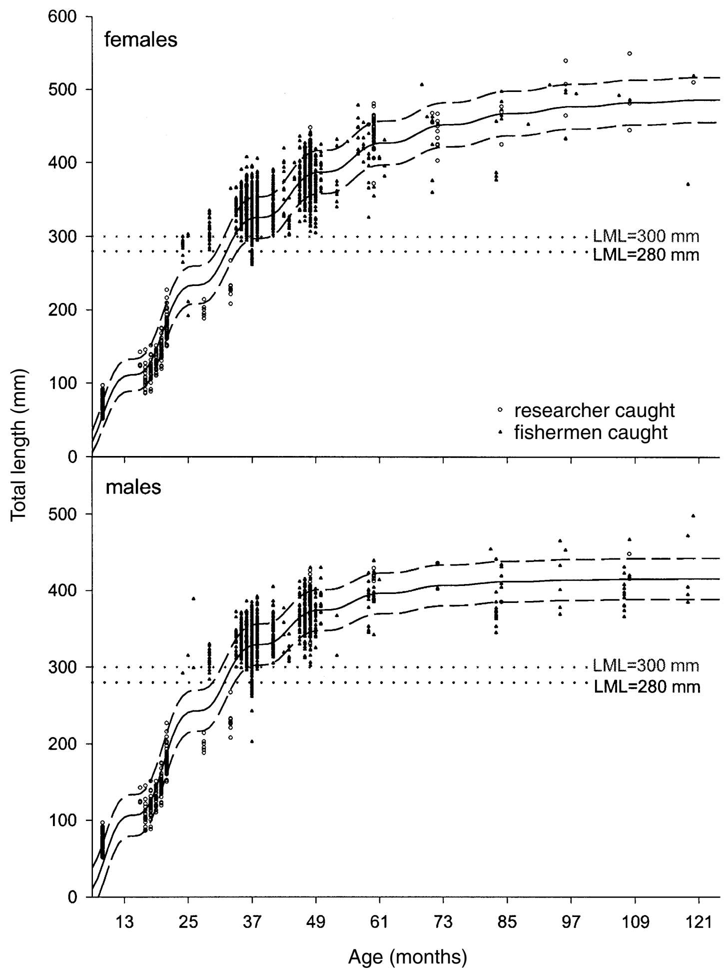

Figure 3

Lengths versus age of King George whiting sampled from Spencer Gulf, plotted as in Figure 2.

ratio tests showed that β did not differ significantly from 3.2 (Table 4). With β = 3.2 fixed, values of α among the six data sets differed little (Table 5, Fig. 7).

Discussion

In this study we estimated parameters of length at age for six data sets, comparing the fits of different models by using four standard diagnostic tools, notably likelihood ratios, correlations, standard errors, and parameter estimates among data sets either varying widely or varying little, to evaluate the estimators being compared. Similarly, for weight versus length in the same population, we assessed six data sets, and used likelihood ratio to compare model fits. For both length at age and weight versus length, the diagnostic analysis suggested the initial full models were overparameterized and indicated which parameters should be fixed and what values.

Likelihood ratio tests allow comparisons only between hierarchical models, that is in comparing full and reduced models, the latter a subcase of the full model obtained by fixing one or more parameters in the full model. In the case of generalized von Bertalanffy and Akamine-Richards, setting r = 1 yielded the same model, namely seasonal von Bertalanffy. The other two reduced models analyzed (gVB with t_0=0 and with both t_0=0 and s_1=0.3) were reduced models only of generalized von Bertalanffy. Although other comparison tests are possible for hierarchical models (Quinn and Deriso, 1999), the Neyman Pearson lemma assures that in the situation where it applies, the likelihood-ratio test is optimal in that it yields the most powerful test for any given choice of significance level, α (Rice, 1995).

Fits of nonhierarchical models can be compared by using the Akaike or Bayes information criteria (Quinn and Deriso, 1999). Fournier et al. (1998) applied the Aitkin posterior Bayes factors for hypothesis model comparisons in

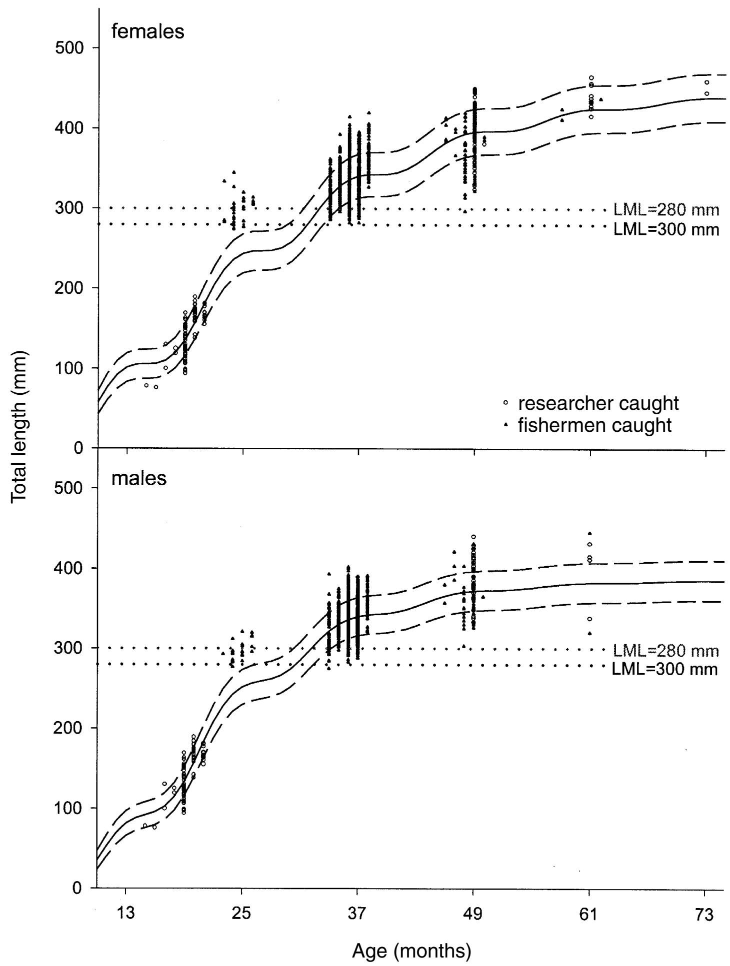

Figure 4

Lengths at age for the South Australian West Coast, plotted as in Figure 2.

a Bayesian context. Recently, Buckland et al. (1997) have proposed averaging the estimates from the range of models examined, weighting each estimate by functions of the Akaike or Bayes information criteria. This mitigates the need to choose one specific model as we have done, and like the Akaike or Bayes criteria, applies to nonhierarchically related models. However, in situations where the growth model will be incorporated into a larger stock assessment estimation, a range of growth submodels would be challenging to implement. Moreover in cases where evidence of overparameterization is given, a reduced-parameter model can reduce both bias and the influence of sample variation.

Sinusoidal seasonality (Pauly and Gaschütz[1]) was represented in a now standard way that preserves the interpretation of t_0 as the age at which length equals zero (Somers, 1988; Hoenig and Hanumara, 1990). Pawlak and Hanumara (1991) showed that this form of seasonality model yielded statistical advantage. Hyndes et al. (1998) aged samples of King George whiting in southwestern Australia that grew faster and reached larger maximum lengths than those from South Australia. The analysis of Hyndes et al. (1998) did not describe the distribution of lengths-at-age or consider seasonality, which was less evident in their plotted data.

The exponent, r, allowed nonlinear variation away from the strict von Bertalanffy form. With the South Australian King George whiting data sets, it improved the model description; fitted r's ranged from 1.25 to 4.59, outside the range describable by the unmodified seasonal von Bertalanffy model where implicitly $r = 1$ fixed.

We are not aware of previous attempts to use a truncated likelihood in an age-based description although Smith and Botsford (1998) applied size truncation in fitting a von Foerster equation to length samples. Truncation proved effective in alleviating this potential large source of bias. The extent of the bias is evident in the growth curve scatterplots (notably Figs. 2 and 4) where large numbers of

Table 3

Length-age parameters and derived estimates (with t_0=0 fixed). The 95% confidence intervals shown in parentheses are 1.96 times the asymptotic standard error; for strictly positive parameters, these are shown as percentages of the estimate value.

	Gulf St. Vincent		Spencer Gulf		West Coast	
Parameter	females	males	females	males	females	males
L_∞	467.0	418.4	492.6	416.1	454.4	387.0
	(±1.5%)	(±1.1%)	(±2.2%)	(±1.5%)	(±3.2%)	(±2.8%)
K	0.48	0.61	0.49	0.77	0.70	1.17
	(±6.4%)	(±5.8%)	(±6.9%)	(±6.6%)	(±9.4%)	(±15%)
u	0.59	0.46	1	1	1	0.79
	(±41%)	(±68%)	(±0.05%)	(±0.08%)	(±0.14%)	(±57%)
ω	–1.55 (Feb)	24.0 (Apr)	8.50 (Dec)	8.67 (Dec)	8.96 (Dec)	9.02 (Jan)
	(±0.77)	(±0.004)	(±0.32)	(±0.39)	(±0.42)	(±0.59)
s_0	8.97	4.17	7.34	27.6	3.53	3.93
	(±58%)	(±47%)	(±52%)	(±53%)	(±96%)	(±100%)
s_1	0.19	0.32	0.23	-0.005	0.35	0.31
	(±0.10)	(±0.082)	(±0.091)	(±0.095)	(±0.17)	(±0.17)
r	1.25	1.41	1.66	2.35	2.33	4.59
	(±6.9%)	(±7.8%)	(±6.9%)	(±9.8%)	(±11%)	(±40%)

Table 4

Likelihood-ratio tests comparing differences in the fits between weight-length models which allow β to vary and those which kept $\beta = 3.2$ fixed. Significant difference is indicated by $P < 0.05$.

	Gulf St. Vincent		Spencer Gulf		West Coast	
	females	males	females	males	females	males
β-estimate (free to vary)	3.200255	3.200008	3.200031	3.198721	3.200050	3.200021
L-ratio statistic	0.677	0.000	0.005	6.094	0.033	0.006
P-significance (models differ)	0.41	0.99	0.94	0.01*	0.86	0.94

Table 5

Weight (g) versus length (mm TL) parameters from Equation 6 and derived estimates with $\beta = 3.2$ fixed. 95% confidence intervals are 1.96 times the bootstrap standard deviation over 1000 runs given in parentheses as percentages of the estimate value.

	Gulf St. Vincent		Spencer Gulf		West Coast	
Parameter	females	males	females	males	females	males
α	$1.858–10^{-6}$	$1.874–10^{-6}$	$1.880–10^{-6}$	$1.888–10^{-6}$	$1.861–10^{-6}$	$1.887–10^{-6}$
	(±0.51%)	(±0.63%)	(±0.77%)	(±0.87%)	(±0.40%)	(±0.32%)
β	3.2	3.2	3.2	3.2	3.2	3.2
σ_{w0}	–7.76	–6.74	–6.94	–5.21	–6.38	–6.32
	(±15%)	(±12%)	(±13%)	(±24%)	(±13%)	(±6.2%)
σ_{w1}	0.094	0.080	0.087	0.078	0.067	0.063
	(±8.0%)	(±7.2%)	(±12%)	(±19%)	(±8.0%)	(±4.6%)

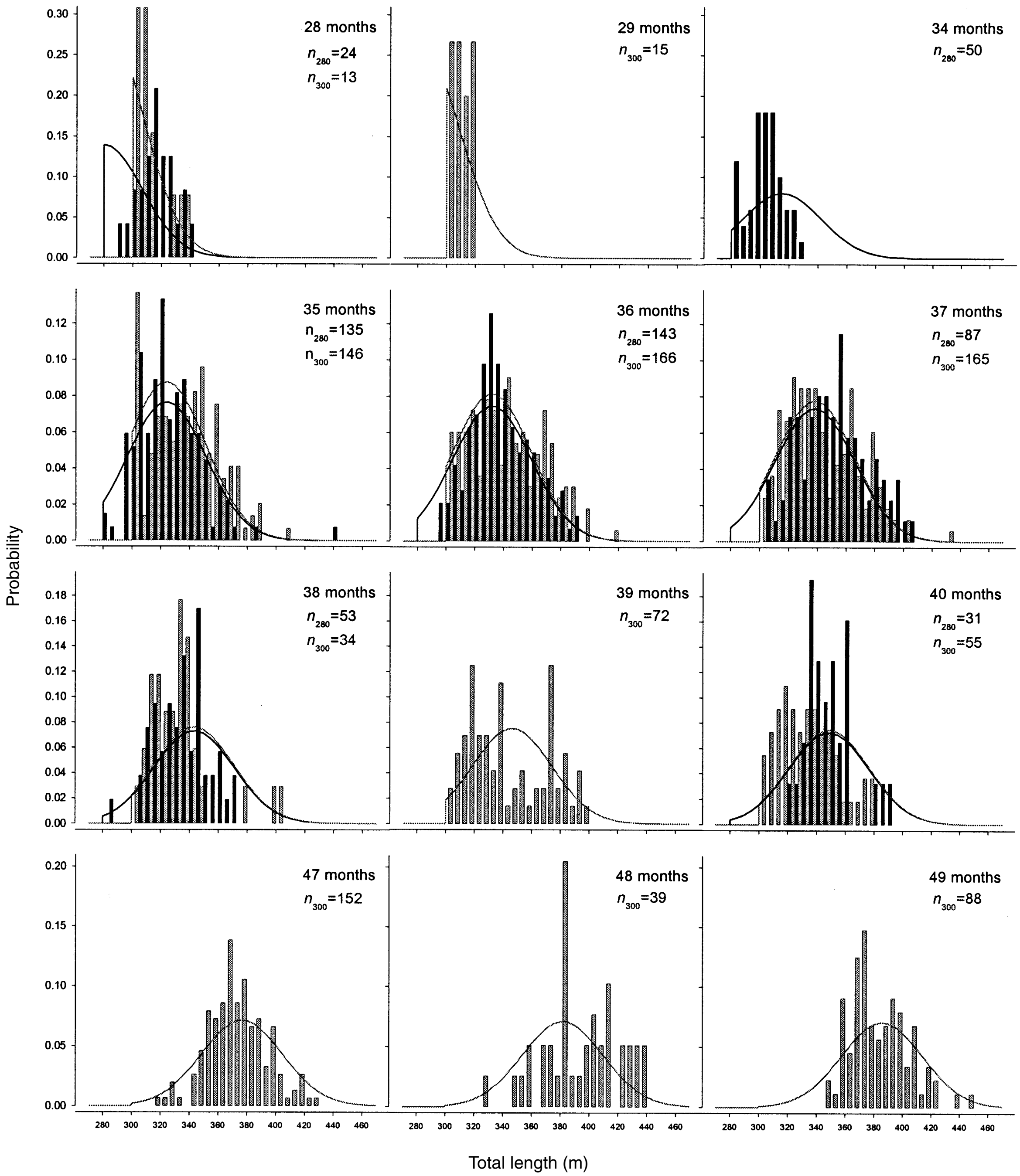

Figure 5

Female Gulf St. Vincent length-frequency histograms expressed as proportion of fish caught per 5-mm length class. Ages (by month) illustrated were those of largest sample size. Black bars correspond to fish caught when the fishery was subject to a 280-mm size limit, and gray bars for fish caught under a 300-mm size limit. The fitted normal likelihood probability density curves (Eq. 4) calculated for each size limit have been overlaid for comparison.

samples were obtained in the ages (~30 months) at which the faster fish are entering the legal-size stock. These clumps of points lie well above the estimated mean length at age. In the absence of the truncation method, the mean curves would pass through these points.

Only the Akamine-Richards model failed to converge with the South Australian King George whiting data sets. Because the Richards form of the model includes both the exponent and its inverse in different places in the formula, it is likely to result in a more numerically challenging

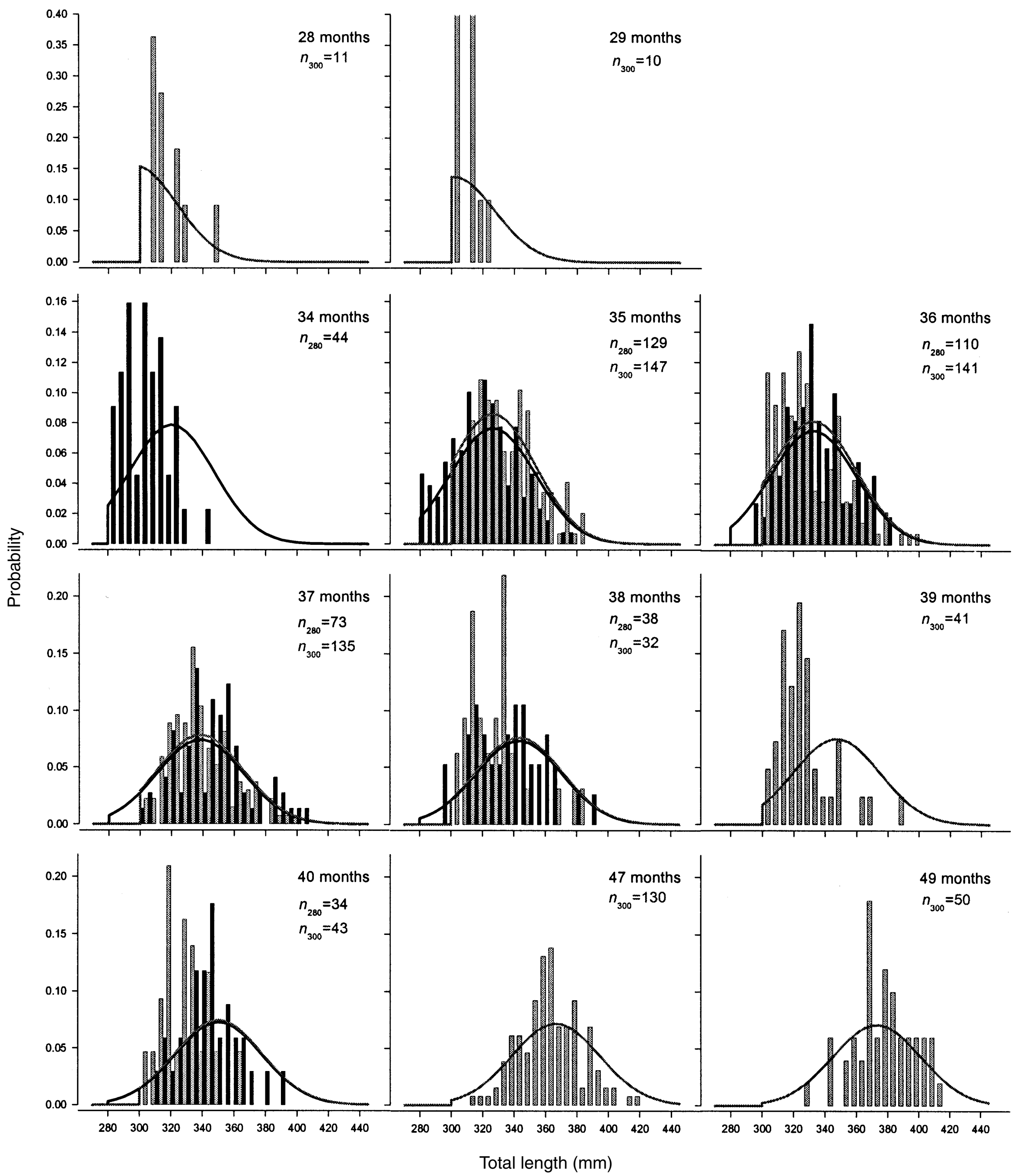

Figure 6

Male Gulf St. Vincent length-frequency histograms and fitted truncated normal density curves, as in Figure 5.

minimization algorithm. The two occurrences of the parameter, r, in the Richards formula $L = L_\infty/\{1 + re^{-K(t-t_0)}\}^{1/r}$, as a factor in front of the negative exponential and as its reciprocal exponent around the entire function apart from L_∞ can act in contrary fashion. For $r > 1$, increases in r imply an increase in length-at-age because of the parameter as a reciprocal exponent, and the opposite for the second role the parameter plays in describing mean length. We speculate that the Richards growth formula was less numerically robust because r can rise and fall at different parameter ranges along the path to convergence, resulting in a more complex likelihood surface.

Modeling the full length distribution at each monthly age is valuable for assessing populations of heavily ex-

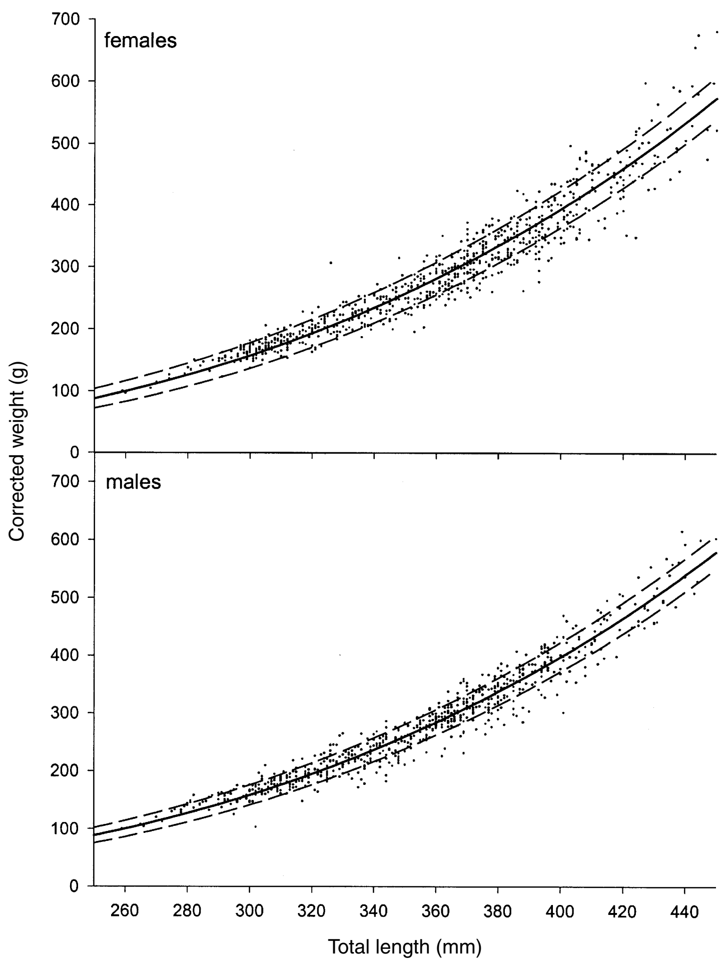

Figure 7

Allometric length versus weight relationship (Eq. 6), fitted to Gulf St Vincent samples. Weights for some fish samples are corrected for the removal of scales before weighing. Error bars (dashed lines) indicate normal likelihood standard deviation (Eq. 7).

ploited species such as King George whiting where depletion of the legal sizes of the cohort is rapid over monthly time scales. In fishery stock assessment models where only legal-size lengths of each yearly cohort are subject to exploitation and where size selection is driven primarily by a legal size limit rather than size-varying gear selectivity, model accuracy is improved by dividing the cohort length distribution into legal and sublegal components.

Growth was variable, reflected in high standard deviations in lengths-at-age of King George whiting. This meant a time span of 12–24 months between the crossing into legal size of the first (i.e. fastest growing, at ~23 months of age) and last 2% of the normal cohort to reach LML. Because fishing mortalities are such that a majority of fish are removed within 24 months of reaching legal size, the explicit representation of the distribution of harvestable lengths of cohorts as they cross LML allows substantial improvements in stock assessment, notably in fitting only legal sizes to monthly catch totals by weight and sampled numbers at age. Moreover, the seasonal variations in fishing effort targeted on South Australian King George whiting appear to track the arrival of the bulk of recruits to legal size in autumn and early winter. The growth model presented in our study allowed this feature of seasonal timing in recruitment to be captured in the associated stock assessment population model.

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