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**Modelling fish growth: model selection, multi-model inference and model selection uncertainty**

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## Abstract

Model selection based on information theory is a relatively new paradigm in biological sciences with several advantages over the classical approaches. The aim of the present study was to apply information theory in the area of modelling fish growth and to show how model selection uncertainty may be taken into account when estimating growth parameters. The methodology was applied for length-age data of four species of fish, taken from the literature. Five candidate models were fitted to each dataset: von Bertalanffy growth model (VBGM), generalized VBGM, Gompertz growth model, Schnute-Richards growth model, and Logistic. In each case, the ‘best’ model was selected by minimizing the small-sample, bias-corrected form of the Akaike information criterion (AIC). To quantify the plausibility of each model, given the data and the set of five models, the ‘Akaike weight’  $w_i$  of each model was calculated. The average model was estimated for each case based on  $w_i$ . Following a multi-model inference (MMI) approach, the model averaged asymptotic length  $\bar{L}_\infty$  for each species was estimated, using all five models, by model averaging estimations of  $L_\infty$  and weighting the prediction of each model by  $w_i$ . In the examples of this study, model selection uncertainty caused a magnification of the standard error of the asymptotic length of the best model (up to 3.9 times) and thus in all four cases estimating  $L_\infty$  from just the best model would have caused overestimation of precision of the asymptotic length. The VBGM, when used for inference, without being the best model, could cause biased point estimation and false evaluation of precision. Model selection uncertainty should not be ignored even if VBGM is the best model. Multi-model inference by model averaging, based on Akaike weights, is recommended for making robust parameter estimations and for dealing with uncertainty in model selection.

Key words: Bertalanffy, Gompertz, growth models, logistic, Schnute-Richards

## 1. Introduction

The process of individual growth in fish is rooted in physiological processes and is the net result of two opposing processes, catabolism and anabolism (Bertalanffy, 1938). For population analysis, expression of the mean individual body growth of fish in a mathematical expression is needed, relating the size of the species to its age (in the present study, length will be used as a measure of size). Several models have been proposed to estimate the mean growth of individual fish in a population, some of these are based on purely empirical relationship, while others have a theoretical basis and are arrived at by differential equations that link the anabolic and catabolic processes.

The most studied and commonly applied model among all the length-age models is the von Bertalanffy growth model (VBGM) (Bertalanffy, 1938). Other commonly used alternatives are the generalized VBGM (Pauly, 1979), the Gompertz growth model (Gompertz, 1825), the logistic model (Ricker, 1975), and the Schnute-Richards model (Schnute and Richards, 1990).

The most common approach in length-age data analyses is to ‘pick’ one model, usually VBGM, based on the shape of the desired curve and on biological assumptions, and fit it to the data. Inference and estimation of parameters and their precision are based solely on that fitted model. Another approach is to fit more than

one model to the data and then use a criterion like minimizing residual sum of squares or maximizing adjusted  $R^2$  to select the ‘best’ model. When the models are nested, a statistical hypothesis testing approach can be used with an F test or with a likelihood ratio test when the probability distribution of the error structure is specified (Quinn and Deriso, 1999).

During the past twenty years, modern statistical science has been moving away from traditional methodologies based on statistical hypotheses testing. In particular, traditional approaches of hypotheses testing, when applied to model selection, have been often found to be mediocre and of limited value (Akaike, 1981) and it is suggested that its application will diminish in future (Burnham and Anderson, 2002). Hypotheses testing schemes are based on arbitrary  $\alpha$  levels (commonly 0.05 or 0.01), multiple testing is challenging, and tests between models that are not nested are problematic. The adjusted coefficient of multiple determination ( $\text{adj-}R^2$ ) that is often used in model selection was found to be a very poor approach (McQuarrie and Tsai, 1998).

Model selection based on information theory is a relatively new paradigm in biological sciences and is quite different from the usual methods based on null hypothesis testing. The basis of the information theory approach to model selection and inference is Kullback-Leibler (K-L) information (or K-L distance),

$$I(f, g) = \int f(x) \log\left(\frac{f(x)}{g(x|\theta)}\right) dx \quad (\text{Kullback and Leibler, 1951}).$$

$I(f, g)$  is the ‘information’ lost when model  $g$  (with parameters  $\theta$ ) is used to approximate full reality or truth  $f$ ; equivalently  $I(f, g)$  is interpreted as the distance from the approximating model to full reality (Burnham and Anderson, 2002). Information theory proposes the minimization of K-L distance as a fundamental basis for model selection. However, K-L distance cannot be computed without knowledge of both full reality  $f$  and the parameters of every candidate model  $g$ . Akaike (1973) devised a method to approximate K-L distance, based on the empirical log-likelihood function. His method, Akaike’s information criterion or AIC, is summarized in the formula  $\text{AIC} = -2 \log(\mathcal{L}(\hat{\theta} | \text{data})) + 2K$ , where  $\log(\mathcal{L}(\hat{\theta} | \text{data}))$  is the numerical value of the log-likelihood at its maximum point,  $\hat{\theta}$  is the vector of the estimated parameters of the model, and  $K$  the number of estimated parameters. It has to be emphasized that AIC is not a ‘test’ in any sense and that, contrary to the use of other criteria like  $\text{adj-}R^2$ , there is a sound theoretical basis for AIC. The derivation of AIC and related issues are given in detail in Burnham and Anderson (2002).

According to the information theory approach, data analysis is taken to mean the integrated process of *a priori* specification of a set of candidate models (based on the science of the problem), model selection based on the principle of parsimony according to AIC, and the estimation of parameters and their precision. The principle of parsimony implies the selection of a model with the smallest possible number of parameters for adequate representation of the data, a bias versus variance tradeoff.

The information theory method frees the researcher from the limiting concept that the proper approximating model is somehow ‘given’. When a model is ‘picked’ in some way, independent of the data, and used to approximate the data as a basis for inference, both the uncertainty associated with model selection and the benefits of selecting a parsimonious model are ignored. This strategy incurs substantial costs in terms of reliable inferences, because uncertainty in model selection is assumed to be zero. If model selection uncertainty is ignored, precision is likely overestimated, estimated confidence intervals of the parameters are often below the nominal level,

and predictions may be less accurate than expected. When the data support evidence of more than one model, model averaging the predicted response variable across models is advantageous in reaching a robust inference that is not conditional on a single model. Rather than estimating parameters from only the ‘best’ model, parameter estimation can be made from several or even all the models considered. This procedure is termed multi-model inference (MMI) and has several theoretical and practical advantages (Burnham and Anderson, 2002). Although there are few instances of the usage of AIC for selection of fish growth models (e.g. Tsangridis and Filippousis, 1994; Imai et al., 2002), there is no instance, to my knowledge, of MMI based on information theory in this field.

In the present article, model selection and MMI based on information theory approach is applied for length-age data. Some examples are given using data from the literature and the results are compared with those where a single model (VBGM) is arbitrarily picked or where a single ‘best’ model is used for inference.

## 2. Methods

### 2.1 Data sets

Four sets of length-age data were taken from the literature: for the yellowfin tuna (*Thunnus albacares*) (both sexes) in the western equatorial Atlantic (Lessa and Duarte-Neto, 2004), for the striped seabream (*Lithognathus mormyrus*) (both sexes) in the Canarian archipelago (Pajuelo et al., 2002), for the male sandbar shark (*Carcharhinus plumbeus*) in the waters of northeastern Taiwan (Joung et al., 2004), and for the rougheye rockfish (*Sebastes aleutianus*) (both sexes) in southeastern Alaska (Quinn and Deriso, 1999). These examples were picked randomly from the literature and were not selected for any desired properties. In the literature, researchers adopt several approaches for data analysis of length-age data. They may use raw observed, raw back-calculated, mean observed (per age class), or mean back-calculated (per age class or per annulus) data. In the examples of the present study, a variety of approaches was applied. To model the data of the rougheye rockfish, average observed lengths of each age class were used, and weighted non-linear least squares (nl-LS) with the sample size of each age class as weights. Mean back-calculated lengths were used for the yellowfin tuna (fork lengths; with weighted nl-LS), while all (for every annulus) mean back-calculated total lengths were used for the sandbar shark (weighted nl-LS) and for the striped seabream (non-weighted nl-LS).

### 2.2 Set of candidate models

A set of five candidate models was used for each dataset to model fish growth: VBGM, generalized VBGM, Gompertz, Schnute-Richards, and Logistic;  $g_1$  to  $g_5$  respectively. The underlying principle of the VBGM is that the growth rate of fish tends to decrease linearly with size, as indicated in the equation  $\frac{dL}{dt} = k_1(L_\infty - L)$ , where  $k_1$  is a relative growth rate parameter (with units  $\text{yr}^{-1}$ ) and  $L_\infty$  is the asymptotic length ( $L_\infty$  has the same biological meaning in all the models described below). The most common parameterization of the solution to the above differential equation is  $L(t) = L_\infty(1 - e^{-k_1(t-t_0)})$ , where  $t_0$  is interpreted as the age when an individual fish would have been of zero length assuming the equation to be valid at all ages. The generalized VBGM is given by the equation  $L(t) = L_\infty(1 - e^{-k_2(t-t_1)})^p$  (Pauly, 1979),

which is equivalent to the Richards equation, expressed as

$$L(t) = L_{\infty} \left( 1 + \frac{1}{p'} e^{-k_3(t-t_2)} \right)^{-p'}$$

that was initially developed by Richards (1959) for plant growth. Richards equation was not included in the set of candidate models to avoid model redundancy. In the generalized VBGM,  $k_2$  and  $t_1$  have similar interpretation as in VBGM, and  $p$  is a dimensionless factor. While the VBGM has no inflection point for  $t > 0$  (its graph is concave downward), the generalized VBGM is sigmoidal having an inflection point at  $t = t_1 + \ln(p)k_2^{-1}$ . The Gompertz growth model (Gompertz, 1825) is an alternative sigmoidal growth curve that assumes exponential decrease of the growth rate with size and is given by the differential equation  $\frac{dL}{dt} = \lambda e^{-k_4 t} L$ , where  $\lambda$

is the theoretical initial relative growth rate at zero age (with units  $\text{yr}^{-1}$ ) and  $k_4$  is the rate of exponential decrease of the relative growth rate with age (with units  $\text{yr}^{-1}$ ). A common parameterization of the solution of this equation is

$$L(t) = L_{\infty} \exp\left(-\frac{1}{k_4} e^{-k_4(t-t_3)}\right), \text{ where } t_3 = \frac{1}{k_4} \ln \lambda \text{ (Quinn and Deriso, 1999).}$$

The inflection point of the Gompertz model appears at  $t = k_4^{-1} \ln(\lambda / k_4)$ . The logistic

model, given by the equation  $L(t) = L_{\infty} \left( 1 + e^{-k_5(t-t_4)} \right)^{-1}$ , is also in use (Ricker, 1975), where  $k_5$  is a relative growth rate parameter (with units  $\text{yr}^{-1}$ ) and  $t_4$  corresponds to the inflection point of the sigmoidal curve. The Schnute-Richards model is a 5-parameter

model, given by the equation  $L(t) = L_{\infty} \left( 1 + \delta e^{-k_6 t^{\nu}} \right)^{1/\gamma}$ , proposed by Schnute and Richards (1990). It provides an omnibus approach to modelling fish growth, and all the aforementioned models are special cases of the Schnute-Richards model with properly selected values for the dimensionless parameters  $\delta$ ,  $\nu$ , and  $\gamma$  (Quinn and Deriso, 1999). The parameter  $k_6$  has units  $\text{yr}^{-\nu}$ .

### 2.3 Modelling growth

The five candidate models  $g_i$  ( $i = 1$  to 5) were fitted to each dataset, with non-linear least squares (nl-LS) with iterations by means of Marquardt's algorithm, assuming additive error structure.

Model selection and the estimation of model selection uncertainty were based on the information theory approach (Burnham and Anderson, 2002). The small-sample, bias-corrected form  $\text{AIC}_c$  (Hurvich and Tsai, 1989; Shono, 2000) of the AIC (Akaike, 1973; Burnham and Anderson, 2002) was used for model selection. Specifically,

$$\text{AIC}_c = \text{AIC} + \frac{2k(k+1)}{n-k-1}, \text{ where for least squares } \text{AIC} = n \log(\hat{\sigma}^2) + 2k, \hat{\sigma}^2 = \text{RSS}/n,$$

$\text{RSS}$  is the residual sum of squares,  $n$  the number of observations, and  $k$  is the total number of estimated regression parameters including  $\sigma^2$  (i.e.  $k$  is the number of parameters in the model equation plus 1). Normally distributed deviations with constant variance were assumed. The model with the smallest  $\text{AIC}_c$  value ( $\text{AIC}_{c,\min}$ ) was selected as the 'best' among the models tested. The  $\text{AIC}_c$  differences,  $\Delta_i = \text{AIC}_{c,i} - \text{AIC}_{c,\min}$  were computed over all candidate models  $g_i$ . According to Burnham and Anderson (2002), models with  $\Delta_i > 10$  have essentially no support and might be omitted from further consideration, models with  $\Delta_i < 2$  have substantial support, while there is considerably less support for models with  $4 < \Delta_i < 7$ . To quantify the plausibility of each model, given the data and the set of five models, the

‘Akaike weight’  $w_i$  of each model was calculated, where  $w_i = \frac{\exp(-0.5\Delta_i)}{\sum_{k=1}^5 \exp(-0.5\Delta_k)}$ . The

‘Akaike weight’ is considered as the weight of evidence in favor of model  $i$  being the actual best model of the available set of models (Akaike, 1983; Buckland et al., 1997; Burnham and Anderson, 2002). ‘Average’ models were determined by averaging the predicted response variable  $L(t)$  across models, using the corresponding  $w_i$ ’s as weights (Burnham and Anderson, 2002).

For each of the five candidate models, the expectation  $\hat{L}_\infty$ , asymptotic standard error  $\text{se}(\hat{L}_\infty)$  and 95% confidence interval (CI) of the asymptotic length were estimated. Asymptotic 95% CI was estimated as  $\hat{L}_\infty \pm t_{df,0.975} \text{se}(\hat{L}_\infty)$ . Following the MMI approach, the model averaged asymptotic length  $\bar{L}_\infty$  was estimated as a weighted average using all five models with the prediction of each model weighted by  $w_i$ . Thus, the model averaged asymptotic length is:

$$\bar{L}_\infty = \sum_{i=1}^5 w_i \hat{L}_{\infty,i} \quad (1)$$

The unconditional standard error of  $\bar{L}_\infty$  was estimated as (Burnham and Anderson, 2002):

$$\text{se}(\bar{L}_\infty) = \sum_{i=1}^5 w_i \left( \text{var}(\hat{L}_{\infty,i} | g_i) + (\hat{L}_{\infty,i} - \bar{L}_\infty)^2 \right)^{1/2} \quad (2)$$

where  $\text{var}(\hat{L}_{\infty,i} | g_i)$  is the variance of the estimated asymptotic length according to model  $g_i$ , conditional on the model.

### 3. Results

For each dataset and for each candidate model the corresponding  $\text{adj-R}^2$ ,  $\text{AIC}_c$ ,  $\Delta_i$ ,  $w_i$ ,  $\hat{L}_{\infty,i}$ ,  $\text{se}(\hat{L}_{\infty,i})$ , and 95% confidence limits of  $\hat{L}_{\infty,i}$  are given in Table 1, as well as the values of  $\bar{L}_\infty$ ,  $\text{se}(\bar{L}_\infty)$ , and 95% confidence limits of  $\bar{L}_\infty$ . The Gompertz model was found to be the best among all the candidate models for the yellowfin tuna. The logistic model was also supported to some extent by the data, while all the other models had considerably less support. VBGM was least supported among the set of candidate models with a weight of evidence of only 1.5%, according to Akaike weights. For the striped seabream, VBGM was found to be the best; the generalized VBGM also had some support, while Gompertz and logistic models had essentially no support. For the sandbar shark, all models except the logistic model were strongly supported by the data, with Gompertz being the best model. For the rougheye rockfish, the generalized VBGM was found to be the best model and Schnute-Richards also had substantial support; the VBGM had almost no support, while Gompertz and the logistic models had essentially no support. The average model and the VBGM for each of the four datasets are shown in Fig. 1.

Adjusted- $\text{R}^2$  did not perform well in model selection, as in three of the four datasets, it predicted a different ‘best’ model than  $\text{AIC}_c$ . The complete ranking of the five models was different when using the criterion of maximum adjusted- $\text{R}^2$  as against when using minimum  $\text{AIC}_c$ , in all four datasets (Table 2).

In many cases, the confidence intervals of  $L_\infty$  for different models of the same dataset did not intersect, indicating significant differences in model predictions (e.g. for the sandbar shark, both VBGM and Gompertz had substantial support but their predictions for  $L_\infty$  differed significantly). The point estimation and the asymptotic 95% CI of  $L_\infty$  for VBGM, the best model, and the average model for each dataset, are given in Fig. 2. The 95% CI for the average model was always wider than for the best model, as it included model selection uncertainty, i.e. the best models overestimated precision. The VBGM overestimated precision when it had substantial support (as in the cases of the striped seabream and the sandbar shark), but could either overestimate (in the rougheye rockfish) or underestimate (in the yellowfin tuna) precision when it did not have substantial support.

#### 4. Discussion

Often, model selection is considered as a method to select just a single ‘best’ model and the subsequent inference and parameter estimation are conditional upon that model. Although this approach is better than the arbitrary picking of a single model without any consideration of alternatives, it is still a simplistic approach that does not fully exploit the potential of information theory. Model selection should not simply be considered as the hunt for a single ‘best’ model; instead, more reliable inferences should be sought based on the entire set of candidate models. In none of the four examples of the present study was the best model strongly supported as a ‘clear winner’ (with  $w_i > 90\%$ ). In each case there was at least one additional model that was also supported by the data. When the data support more than one model, there is substantial degree of uncertainty in model selection that cannot be ignored. Due to model selection uncertainty, there is often a non-negligible variance component that would cause overestimation of precision, if ignored. Burnham and Anderson (2002) presented some examples of Monte Carlo simulations to evaluate unconditional sampling variance estimation, confidence intervals, and model averaging. They found in their simulations that incorporating model selection uncertainty by model-averaging (for model selection under  $AIC_c$ ) can bring achieved confidence interval coverage up to approximately the nominal level and that unconditional confidence interval coverage is much superior to conditional coverage.

In the examples of this study, model selection uncertainty caused a magnification of the standard error of the asymptotic length (of the best model), from 1.4 times for the yellowfin tuna up to 3.9 times for the rougheye rockfish. Thus in all the examples, adopting the best model would probably cause overestimation of precision of the asymptotic length. Unconditional variance (i.e. not conditional on a particular model) is still conditional on the full set of candidate models. If all the models considered *a priori* are not carefully selected based on the science of the problem, then the precision of the parameters might still be overestimated.

It has to be emphasized that the results of an information-theoretic approach depend on the set of the candidate models. The published literature, experience in the biological sciences, and critical thinking should be used to formulate the set of *a priori* candidate models. As Chatfield (1995) suggested, there is a need for careful and critical thinking and the emphasis should not be focused on the analysis theory with too little thought of the real biological question. Model formulation is the point where the biological information formally enters the investigation. It is partially a subjective art and conceptually more difficult than just estimating the model parameters and their

precision. In developing the set of candidate models, one must recognize a certain balance between keeping the set small and focused on plausible hypotheses, while making it big enough to guard against omitting a very good a priori model (Burnham and Anderson, 2002). Using AIC or other similar methods, one just hopes to select the best model (or models) from the set of candidate models; if good models are missing from the set of candidate models, they cannot be discovered by any model selection methodology.

To illustrate that the resultant model-averaged estimates depend on the set of candidate models, for the sandbar shark dataset, the Schnute-Richards model (which was the second best model with  $w_i = 30.5\%$ ) was eliminated and AIC<sub>c</sub> differences, Akaike weights, and model-averaged estimates were re-calculated. The results (Table 3) are quite different to those when the full set of five models was used; only one model had substantial support by the data with  $w_i = 99\%$ , asymptotic length was slightly reduced, and unconditional standard error was substantially reduced by a factor of 3.9.

Although VBGM is the most studied and commonly applied model among all length-age models, its *a priori* use as the unique growth model is not a good practice. VBGM was selected as the best model only in one of the four cases examined (for the striped seabream), while it had considerably less support than the selected models in two of the cases (for the yellowfin tuna and the rougheye rockfish). The VBGM, when used for inference, without being the best model, could cause biased point estimation and false evaluation of precision (as in the cases of the yellowfin tuna, the sandbar shark, and the rougheye rockfish; Fig. 2). Even if VBGM is the best model, model selection uncertainty should not be ignored.

In the present study,  $L_\infty$  was chosen to demonstrate MMI but any other parameter or model-predicted quantity could be model-averaged in the same manner.

For example, if growth rate at a specific age  $T$  needed estimation, the quantity  $\left. \frac{dL}{dt} \right|_{t=T}$  would be estimated from each model by differentiation. The model-averaged growth rate would then be estimated by Eq. 1 and the corresponding unconditional standard error by Eq. 2, replacing  $L_\infty$  with  $\left. \frac{dL}{dt} \right|_{t=T}$  and estimating conditional variances e.g. with non-parametric bootstrap (Efron and Tibshirani, 1993). Parameters  $k_i$  and  $t_i$  do not have the same meaning in all the models of the present study and may not be model averaged.

Bayesian methods in model selection and inference have also been the focus of much recent research and could also be used in modelling fish growth. Bayesians, under different approaches and assumptions, have proposed several alternative methods for model selection, e.g. Bayesian Information Criterion BIC, as well as full Bayesian model selection (e.g. Hoeting et al. 1999). Such approaches, although being in the state of the art in statistics, may seem difficult for biologists to implement due to their high technical level and are also quite often computationally demanding. On the contrary, an information-theoretic approach is quite simple to implement and not computer intensive. There is also a different philosophical base for the two approaches. The full Bayesian approach generally seems to assume that one of the candidate models  $g_i$  is ‘true’, and prior probability of  $g_i$  is the prior degree of belief that the specific model is the true one. Under the information-theoretic approach it is not assumed that truth  $f$  is included in the set of models and the issue is not which model is true, but rather which model when fit to the data is the best one for

representing the finite information contained in the data. The concept of a ‘true’ model seems to be of little utility in the biological sciences. Biological systems are quite complex with many small effects (tapering effects), individual heterogeneity, and interactions that are generally unknown. On an information-theoretic approach, ‘information’ about the biological system under study exists in the data and the goal is to express this information in a compact way; the more data available the more information exists, i.e. a more complicated model may approximate the data. Burnham and Anderson (2002) showed that AIC can be justified as a Bayesian model selection criterion with model prior proportional to  $\exp(0.5k \log(n) - k)$  (while BIC assumes a uniform prior distribution). Consequently, Akaike weights may be interpreted as a posterior probability distribution over the model set (i.e.  $w_i$  is the probability that model  $g_i$  is the K-L best model) and AIC is ‘Bayesian’ to the same extent as BIC; a detailed discussion is given in Burnham and Anderson (2002).

## 5. Conclusion

Model selection based on information theory is recommended for studying growth, as an effective method in finding a parsimonious approximating model. Multi-model inference by model averaging, based on Akaike weights, is recommended for making robust parameter estimations and dealing with model selection uncertainty.

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Table 1: For each dataset and for each candidate model,  $\text{adj-R}^2$ , the small-sample bias corrected form of Akaike’s information criterion  $\text{AIC}_c$ , Akaike differences  $\Delta_i$ , Akaike weights  $w_i$ , and the estimation of asymptotic length  $L_\infty$  with the corresponding conditional asymptotic standard error (se), and 95% conditional confidence limits (CL). Point estimation, se, and 95% CL for the model-averaged asymptotic length are also given (unconditional estimations). The models are sorted from best to worst. VBGM is the Von Bertalanffy Growth Model;  $k$  is the total number of estimated regression parameters in the model.

models	$k$	adj-R <sup>2</sup>	AIC <sub>c</sub>	$\Delta_i$	$w_i$	Asymptotic length (cm)				
						point estimation	se	95% CL		
							lower	upper		
<b>yellowfin tuna (both sexes)</b>										
<b>g<sub>3</sub></b>	Gompertz	4	0.9936	82.94	0.00	77.4%	198.86	4.84	188.07	209.65
<b>g<sub>5</sub></b>	Logistic	4	0.9920	85.87	2.93	17.9%	188.47	3.69	180.24	196.69
<b>g<sub>2</sub></b>	generalized VBGM	5	0.9929	89.64	6.70	2.7%	199.48	9.75	177.43	221.52
<b>g<sub>1</sub></b>	VBGM	4	0.9883	90.80	7.86	1.5%	233.12	15.66	198.23	268.01
<b>g<sub>4</sub></b>	Schnute-Richards	6	0.9923	93.32	10.37	0.4%	193.32	23.26	139.69	246.96
<b>Model-Averaged</b>							<b>197.51</b>	<b>6.61</b>	<b>182.80</b>	<b>212.23</b>
<b>striped seabream (females)</b>										
<b>g<sub>1</sub></b>	VBGM	4	0.9970	21.96	0.00	72.7%	40.74	0.67	39.39	42.10
<b>g<sub>2</sub></b>	generalized VBGM	5	0.9977	24.45	2.49	20.9%	41.66	2.34	36.88	46.44
<b>g<sub>4</sub></b>	Schnute-Richards	6	0.9976	27.22	5.26	5.2%	42.18	5.98	29.98	54.37
<b>g<sub>3</sub></b>	Gompertz	4	0.9971	30.24	8.28	1.2%	37.53	0.44	36.63	38.42
<b>g<sub>5</sub></b>	Logistic	4	0.9958	43.93	21.97	0.0%	35.94	0.39	35.15	36.73
<b>Model-Averaged</b>							<b>40.97</b>	<b>1.38</b>	<b>38.15</b>	<b>43.79</b>
<b>sandbar shark (males)</b>										
<b>g<sub>3</sub></b>	Gompertz	4	0.9287	13179.55	0.00	31.0%	193.93	0.96	192.05	195.81
<b>g<sub>4</sub></b>	Schnute-Richards	6	0.9288	13179.58	0.03	30.5%	191.92	3.32	185.41	198.43
<b>g<sub>1</sub></b>	VBGM	4	0.9288	13180.49	0.94	19.3%	199.46	1.26	196.99	201.93
<b>g<sub>2</sub></b>	generalized VBGM	5	0.9287	13180.53	0.98	19.0%	195.98	2.45	191.18	200.78
<b>g<sub>5</sub></b>	Logistic	4	0.9284	13189.14	9.59	0.3%	190.29	0.79	188.74	191.84
<b>Model-Averaged</b>							<b>194.77</b>	<b>3.20</b>	<b>188.50</b>	<b>201.03</b>
<b>roughey rockfish (both sexes)</b>										
<b>g<sub>2</sub></b>	generalized VBGM	5	0.9780	427.81	0.00	52.6%	58.71	2.17	54.38	63.04
<b>g<sub>4</sub></b>	Schnute-Richards	6	0.9782	428.05	0.23	46.8%	63.18	14.48	34.29	92.07
<b>g<sub>1</sub></b>	VBGM	4	0.9754	436.92	9.10	0.6%	54.88	0.88	53.12	56.64
<b>g<sub>3</sub></b>	Gompertz	4	0.9699	449.12	21.31	0.0%	51.67	0.77	50.13	53.21
<b>g<sub>5</sub></b>	Logistic	4	0.9638	462.55	34.74	0.0%	52.20	0.73	50.74	53.66
<b>Model-Averaged</b>							<b>60.78</b>	<b>8.48</b>	<b>43.86</b>	<b>77.71</b>

Table 2: Ranking of the five competing models (from best to worst) based on maximizing adjusted  $R^2$  or on minimizing the small-sample bias corrected form of Akaike's information criterion  $AIC_c$ , for each of the four datasets.

yellowfin tuna		striped seabream		sandbar shark		rougheye rockfish	
$AIC_c$	adj- $R^2$	$AIC_c$	adj- $R^2$	$AIC_c$	adj- $R^2$	$AIC_c$	adj- $R^2$
$g_3$	$g_3$	$g_1$	$g_2$	$g_3$	$g_4$	$g_2$	$g_4$
$g_5$	$g_2$	$g_2$	$g_4$	$g_4$	$g_1$	$g_4$	$g_2$
$g_2$	$g_4$	$g_4$	$g_3$	$g_1$	$g_3$	$g_1$	$g_1$
$g_1$	$g_5$	$g_3$	$g_1$	$g_2$	$g_2$	$g_3$	$g_3$
$g_4$	$g_1$	$g_5$	$g_5$	$g_5$	$g_5$	$g_5$	$g_5$

Table 3: Results of modelling growth of the rougheye rockfish, after eliminating the Schnute-Richards model from the original set of candidate models. Abbreviations are as in Table 1.

models	$k$	$AIC_c$	$\Delta_i$	$w_i$	Asymptotic length (cm)				
					point estimation	se	lower	upper	
<b>rougheye rockfish (both sexes)</b>									
$g_2$	gener. VBGM	5	427.81	0.00	99.0%	58.71	2.17	54.38	63.04
$g_1$	VBGM	4	436.92	9.10	1.0%	54.88	0.88	53.12	56.64
$g_3$	Gompertz	4	449.12	21.31	0.0%	51.67	0.77	50.13	53.21
$g_5$	Logistic	4	462.55	34.74	0.0%	52.20	0.73	50.74	53.66
<b>Model-Averaged</b>						<b>58.67</b>	<b>2.19</b>	<b>54.30</b>	<b>63.04</b>

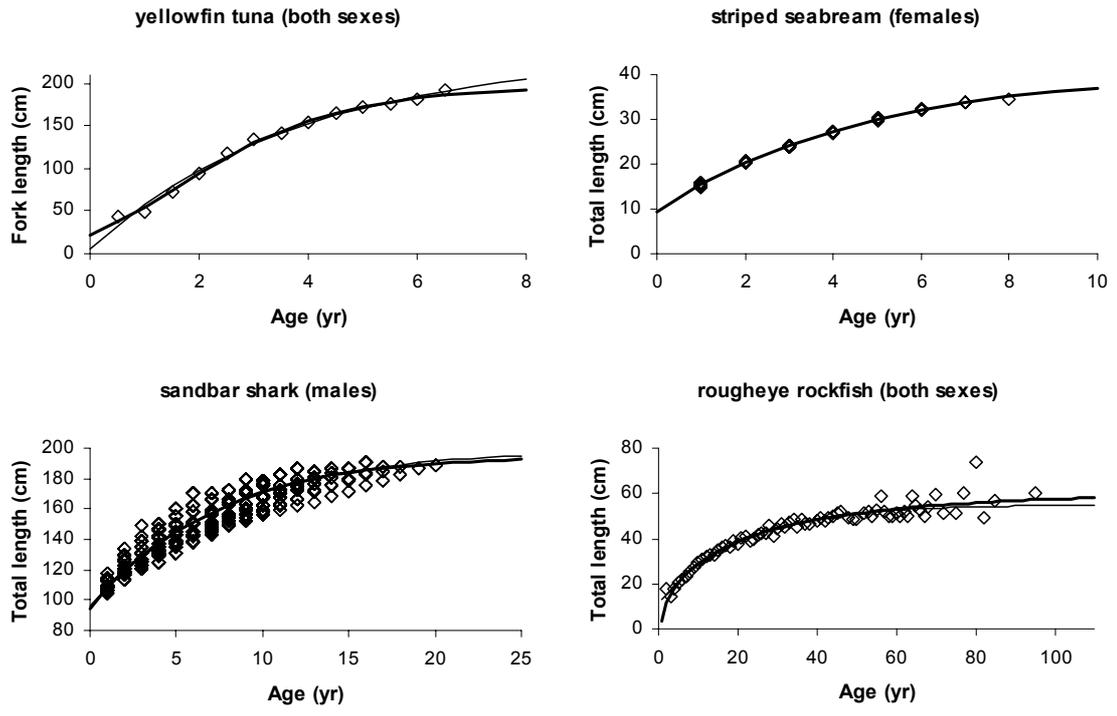


Fig. 1: The average model (solid line) and the von Bertalanffy growth model VBGM (light line) of the four length-age datasets.

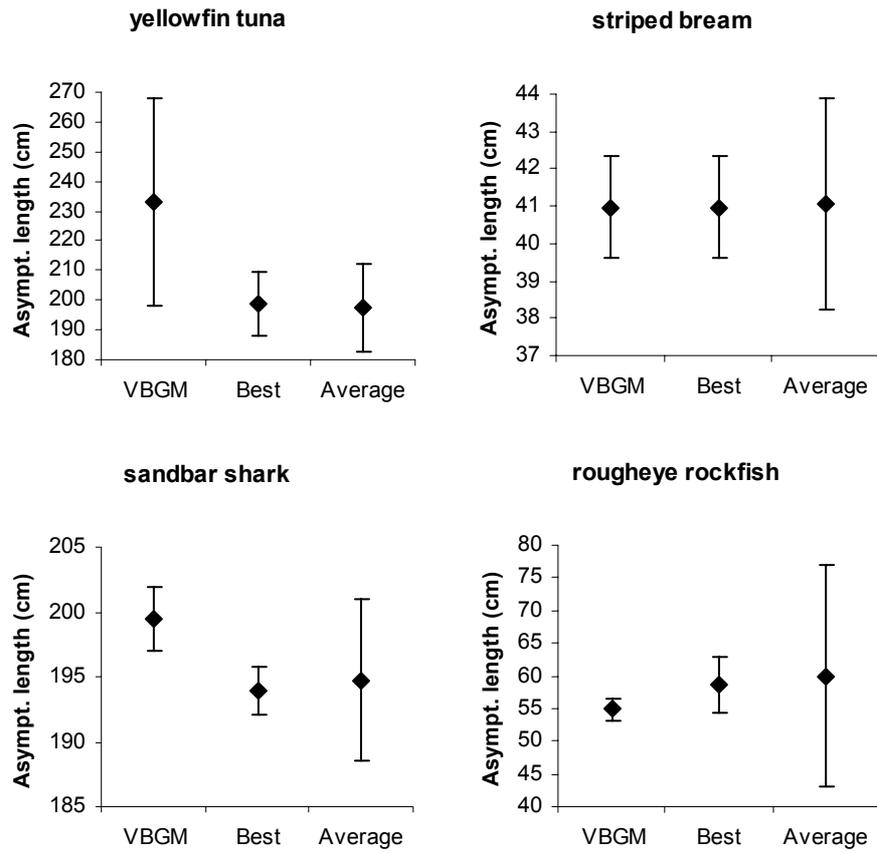


Fig. 2: The point estimation of the asymptotic length  $L_{\infty}$  and the corresponding asymptotic 95% confidence intervals for VBGM (von Bertalanffy growth model), best model, and average model, for each dataset.