

Avoiding fishy growth curves

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Summary

1. Somatic growth is a fundamental property of living organisms, and is of particular importance for species with indeterminate growth that can change in size continuously throughout their life. For example, fishes can increase in size by 2–6 orders of magnitude during their lifetime, resulting in changes in production, consumption and function at the ecosystem scale. Within species, growth rates are traded off against other life-history parameters, hence an accurate description of growth is essential to understand the comparative demography, productivity, fisheries yield and extinction risk of populations and species.

2. The growth trajectory of indeterminate growing sharks and rays (elasmobranchs) and bony fishes (teleosts) is usually modelled using a three-parameter logarithmic function, the von Bertalanffy growth function (VBGF), to describe the total length of the average individual at any given age. Recently, however, a two-parameter form has gained popularity. Rather than being estimated in the model fitting process, the third y-intercept parameter (L_0) of the VBGF has been interpreted as being biologically equivalent to, and thus fixed as, the empirically estimated size at birth.

3. We tested the equivalence assumption that L_0 is the same or similar to size at birth by comparing empirical estimates of size at birth available from the literature with estimates of L_0 from published data from elasmobranchs, and found that even though there is an overlap of values, there is a high degree of variability between them.

4. We calculate the bias in the growth coefficient (k) of the VBGF by comparison between the two- and three-parameter estimation methods. We show that slight deviations in fixed L_0 can cause considerable bias in growth estimates in the two-parameter VBGF while providing no benefit even when L_0 matches the true value. We show that the effect of this biased growth estimate has profound consequences for fisheries stock status.

5. We strongly recommend the use of the three-parameter VBGF and discourage use of the two-parameter VBGF because it results in substantially biased growth estimates even with slight variations in the value of fixed L_0 .

Key-words: conservation, modelling, *Carcharhinus*, Chondrichthyes, life history invariant, fisheries stock assessment, natural mortality

Introduction

Growth is one of the most important measurable life-history parameters for individuals and species (Austin *et al.* 2011; Einum, Forseth & Finstad 2012; Paine *et al.* 2012). Recent comparative and analytical work has shown that understanding growth is fundamental to understanding life histories, demography, ecosystem dynamics, and fisheries sustainability (Beddington & Kirkwood 2005; Frisk, Miller & Dulvy 2005). Across species, growth correlates with a number of life-history traits including natural mortality rate (Pauly 1980; Charnov, Gislason & Pope in press), lifespan (Hoenig 1983) and reproductive allocation (Lester, Shuter & Abrams 2004; Charnov 2008); traits that also influence the response of species to exploitation (Jennings, Reynolds & Mills 1998; Frisk, Miller & Dulvy 2005).

A widely used method of describing growth, currently utilised in at least 100 published articles in each of the last 6 years, is the von Bertalanffy growth function, or VBGF (von Bertalanffy 1938, 1957). This model has been used to describe the change in body size over time of fossil and modern species across a wide range of taxa, including mammals (English, Bateman & Clutton-Brock 2012), birds (Tjørve & Tjørve 2010), reptiles (including dinosaurs) (Lehman & Woodward 2008), amphibians (Arntzen 2000), but it is most extensively applied across the most speciose vertebrate taxon – the fishes (Chen, Jackson & Harvey 1992; Frisk, Miller & Fogarty 2001). Most fisheries stock assessment models rely on von Bertalanffy growth models to convert between population numbers and biomass.

Von Bertalanffy hypothesised that net growth, i.e. the change in mass over time resulting from the difference between anabolism and catabolism, is approximately a one-third power function of size describing the net effect of both metabolic pro-

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cesses. By integrating and converting to a length formulation (assuming weight is proportional to the third power of length) von Bertalanffy defined growth in length as:

$$L(t) = L_{\infty} - (L_{\infty} - L_0)e^{-kt} \quad \text{eqn 1}$$

where $L(t)$ is length-at-age t (age in years, length in cm), L_{∞} is the asymptotic size (in cm), k is the growth coefficient (in yr^{-1}) and L_0 is the length-at-age zero (in cm) (Fig. 1a). While asymptotic size (L_{∞}) is the maximum theoretical size that a species will tend towards, but never actually reach, the growth coefficient (k) is the rate at which growth approaches this asymptote such that it takes $\ln 2 k^{-1}$ units of time to grow halfway towards L_{∞} at any given point (Fabens 1965). The third parameter used in the von Bertalanffy growth equation is the size-at-age zero (L_0) which equates to the y-intercept. Note that two key parameters often lie well beyond the data (the smallest theoretical size L_0 and the largest asymptotic theoretical size L_{∞}). Von Bertalanffy growth models are fitted to empirical length-at-age data (in fishes age is usually estimated from tree ring-like growth checks in the otoliths, vertebrae or spines), with age on the x -axis and length on the y -axis, and models are fit using nonlinear sum-of-squares fitting methods (Appendix I). Some teleost age and growth studies also fix the intercept to zero (McGarvey &

Fowler 2002; Taylor, Walters & Martell 2005; Gwinn, Allen & Rogers 2010), but the two-parameter von Bertalanffy growth function is most widely applied to elasmobranchs as they tend to have a large size at hatch or at birth.

Elasmobranchs, like most fishes, grow continuously and asymptotically throughout their lives and their growth is well-described by the von Bertalanffy model (Beverton & Holt 1959; Cailliet *et al.* 2006). In a recent review of elasmobranch age and growth studies, Cailliet *et al.* (2006) recommended the use of the von Bertalanffy growth function based on the L_0 parameter. This formulation then allows fixing L_0 to a known value, the empirical size at birth, and presents the opportunity to save one degree of freedom in the model fitting process. The key assumption is that the L_0 parameter (better described as the theoretical average length when age is zero) is identical to, and can be replaced by, an empirical estimate of size at birth. As a consequence, the two-parameter von Bertalanffy growth function only requires the estimation of the remaining growth parameters L_{∞} and k from the available length-at-age data. The use of this two-parameter von Bertalanffy growth function has proliferated in recent years (Neer, Thompson & Carlson 2005; Braccini *et al.* 2007; Pierce & Bennett 2010). While there are specific situations where fixing model parameters may

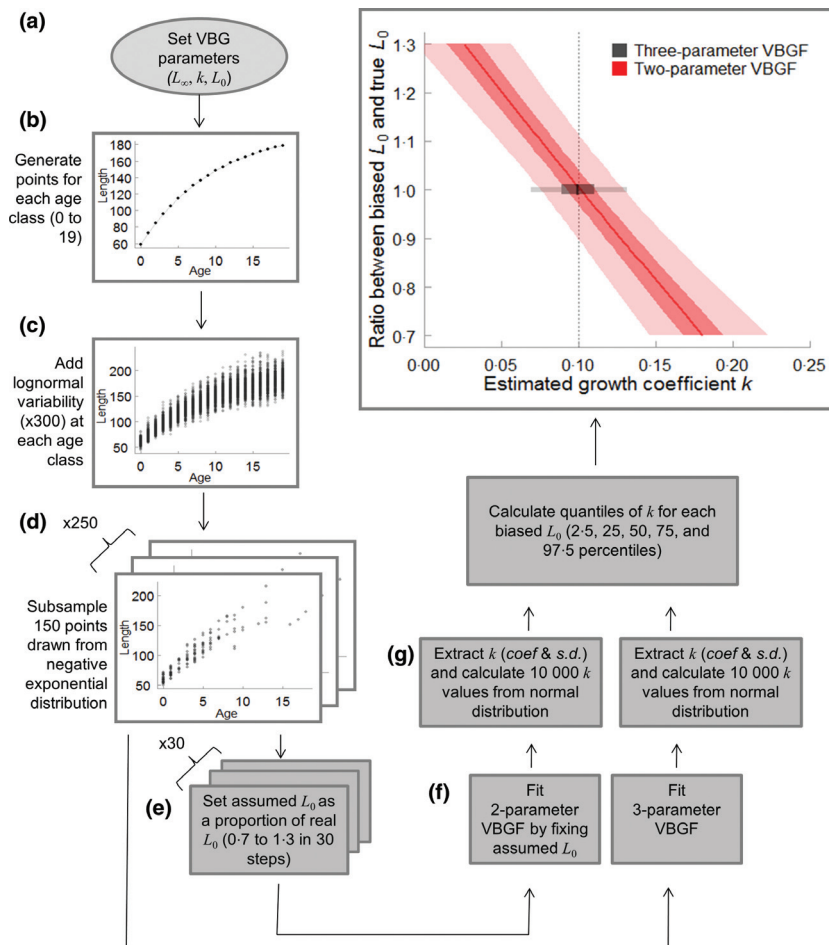


Fig 1. Flow diagram of simulation model created for assessing the effect of fixing the L_0 parameter on the estimation of growth coefficient k in the von Bertalanffy growth function.

improve growth estimates, such as the case of fledgling growth (Tjörve & Tjörve 2010; Austin *et al.* 2011), the consequences of fixing parameters on model performance in the von Bertalanffy growth function have only rarely been examined. A recent comparison of growth models showed that and even though the two-parameter von Bertalanffy growth model was overall the most parsimonious model (i.e. best ranked using Akaike Information Criteria, or AIC), it appears to perform better, with lower estimating error, only in data-sparse simulations compared to the three-parameter variant which performs best in data-rich settings (Thorson & Simpfendorfer 2009).

In addition to fitting two- and three-parameter von Bertalanffy growth models there is an emerging practice of fitting multiple models (both von Bertalanffy models as well as others, such as Gompertz and logistic), comparing them using (AIC), and reporting parameter estimates of all candidate models or a single set of estimates from multi-model averaging (Katsanevakis 2006; Katsanevakis & Maravelias 2008; Thorson & Simpfendorfer 2009). This approach addresses the question of which model is most parsimonious with the available data, trading off model complexity with goodness-of-fit. Unfortunately, a model can be the most parsimonious while still incorrectly describing the underlying growth trajectory. In this study, we test the performance not by the parsimony approach of AIC, but instead by determining whether the two- or the three-parameter von Bertalanffy growth model provides parameter estimates that are closest to the true (simulated) values.

The specific aims of this study were: (1) to test the equivalence assumption that L_0 is the same or similar to empirically estimated size at birth, (2) to compare, in terms of bias and uncertainty, the estimation of the growth coefficient (k) between the two- and three-parameter estimation methods of the von Bertalanffy growth function in data-rich as well as data-sparse scenarios, and (3) to determine whether these differences vary across a range of life histories. We show that L_0 is not equivalent to size at birth, and that assuming so results in severely biased growth estimates, which in turn adversely biases understanding of fisheries stock status. This case study provides a general caution against fixing parameters to save one degree of freedom, especially when the underlying parameters covary.

Materials and methods

First, we assessed the relevance of our analyses by comparing literature estimates of empirical size at birth with estimates of L_0 from published data from elasmobranchs. Second, to evaluate the performance of the two-parameter von Bertalanffy growth model when L_0 is uncertain, we simulated a length-at-age data set for a hypothetical ground shark (*Carcharhinus* sp.) from which we subsampled points with replacement (bootstrap), and then fitted the three growth models to each bootstrap sample and calculated a range of k values. For the two-parameter models, we systematically varied L_0 as a proportion of the true value of L_0 , i.e. the L_0 value used to create the simulated length-at-age data. Third, we generalise our finding across a wider range of life histories by running our analyses using covarying combinations of simulated k , L_∞ and L_0 values.

COMPARISON OF OBSERVED SIZE AT BIRTH AND ESTIMATED L_0

Published empirical size at birth estimates were compared with L_0 estimates for 30 elasmobranch species from 12 families. Bias was defined as the ratio of size at birth and L_0 (i.e. size at birth/ L_0), with high values >1 indicating empirical size at birth is greater than the statistical parameter and *vice versa*. This analysis is not a direct measure of the actual bias in published growth studies, but rather the potential bias that might arise if the available species-level empirical size at birth estimates were substituted for the L_0 parameter.

Estimates of von Bertalanffy growth parameters were obtained from a database search in ISI Web of Science using the following search terms (elasmobranch, shark, skate, ray and chimaera in combination with age, growth, demography and age determination), combined with manual searches of references cited in these articles. We retained only those parameter estimates from wild-caught specimens (not aquarium studies), and only where asymptotic size L_∞ , growth coefficient k and either theoretical age-at-length zero t_0 or length-at-age zero L_0 were estimated. Where possible, we used growth parameters for both sexes combined, and used females' estimates if sexes were separated. Parameter estimates were retained for equations computed from both observed and back-calculated data. If t_0 was estimated instead of L_0 , we calculated the latter using the following equation:

$$L_0 = L_\infty(1 - e^{kt_0}) \quad \text{eqn 2}$$

where k , L_∞ and t_0 are the von Bertalanffy growth parameters. Estimates of size at birth were obtained from a life-history data base compiled by NKD, containing all records of elasmobranch size at birth in elasmobranchs published in the literature up to the year 2008, and are based primarily on the Food and Agriculture Organisation Fisheries Synopses (Compagno 1984a,b).

DATA CREATION THROUGH SIMULATION

We simulated a length-at-age data set for a hypothetical ground shark (which closely resembles the life history of the spinner shark *Carcharhinus brevipinna*) from which we bootstrapped points. The simulated data set consisted of 300 length-at-age estimates for each of 20 age classes, totalling 6000 data points.

First, we created a von Bertalanffy growth curve for our hypothetical elasmobranch species with growth coefficient $k = 0.1 \text{ yr}^{-1}$, asymptotic size $L_\infty = 200 \text{ cm}$, $L_0 = 59.06 \text{ cm}$ (equivalent to $t_0 = -3.5$ years) and $T_{\max} = 19$ years (Fig. 1a,b; Carlson & Baremore 2005).

Second, to simulate uncertainty in size-at-age values, for each of the 20 age classes, we drew 300 random draws from a log-normal distribution with bias correction centred on the mean (Fig. 1c) (Hilborn & Mangel 1997):

$$L_{te} = L_t \times e^{\mathcal{N}(\mu, \sigma) + \frac{\sigma^2}{2}} \quad \text{eqn 3}$$

where L_{te} is the distribution of lengths at age t with error included, L_t is length-at-age t from the original model and $\mathcal{N}(\mu, \sigma)$ is a normal distribution with a mean of 0 (μ) and a standard deviation (σ) of 0.1.

Third, from this simulated data set, we drew 250 samples (with replacement) of 150 points each, using a negative exponential probability distribution (Fig. 1d). This distribution was used to approximate the observed distribution of size frequencies of length-at-age data as expected for a population where mortality is constant (there are always more juveniles than adults).

For each subsample, three variants of the von Bertalanffy growth function were fitted by nonlinear least squares using the *nls* function

(Appendix 1) in R version 2.14.2 (R Development Core Team 2012): (i) a three-parameter VBGF (ii) the modified two-parameter VBGF where average length-at-age zero (L_0) is fixed or set to the empirical size at birth, and (iii) a version of the two-parameter VBGF where the L_0 is fixed iteratively from a normal distribution of possible sizes at birth based on the methodology outlined by Neer, Thompson & Carlson (2005). In the three-parameter model, all three von Bertalanffy growth parameters (k , L_∞ and L_0) are estimated in the equation; however, in both two-parameter variants of the VBGF, the L_0 is fixed, or drawn iteratively from a known normal distribution in each subsample. In the case of the two-parameter growth models, the value of the L_0 parameter used in both two-parameter von Bertalanffy growth function was systematically fixed as a proportion of real L_0 (over the range from 0.7–1.3) to assess the effect of fixing L_0 [hereafter referred to as assumed L_0 (Fig. 1e,f)]. Values were calculated at 0.01 intervals between 0.85 and 1.15 and at 0.05 intervals at the remainder of assumed L_0 values. Both two-parameter formulations of the von Bertalanffy growth model produced very similar growth estimates, hereafter we only compare the version where L_0 is replaced with a single empirical estimate of L_0 .

To assess the bias of the models, 20 000 random draws of the estimated growth coefficients k were taken from normal distributions, which were then compared with the real estimate of k (Fig. 1g). Median values, 50% and 95% quantiles were calculated from the pooled coefficients in each variant of the von Bertalanffy growth function.

HOW DOES THE TWO-PARAMETER VBGF PERFORM WITH SPARSE DATA?

We measured performance under two common data scenarios and an extreme one: (1) a data-rich scenario, in which a total of 150 length-at-age points are subsampled across all age classes; (2) a data-sparse where only 20 length-at-age points are subsampled across all age classes (hereafter referred to as 'thinned scenario'); and (3) a second data-sparse scenario in which 20 length-at-age points are subsampled excluding the youngest three age classes (ages 0–2; hereafter referred to as 'thinned/no-juveniles scenario') (Fig. 1d).

DOES PERFORMANCE OF THE TWO-PARAMETER VBGF VARY ACROSS A RANGE OF LIFE HISTORIES?

Our initial performance analysis focused on a species with a relatively slow life history (i.e. slow growth rates and large size; $k = 0.1 \text{ yr}^{-1}$ and $L_\infty = 200 \text{ cm}$ respectively). Rather than comparing two species with contrasting life histories (Thorson & Simpfendorfer 2009), we expanded our simulation to cover a broader range of life histories for species with growth rates ranging from $k = 0.09$ (slow) to 0.54 yr^{-1} (fast) and asymptotic sizes ranging for $L_\infty = 70$ –225 cm (see Table S1). To do this, we need to understand the degree to which the von Bertalanffy growth parameters covary. Therefore, we modelled the covariance between von Bertalanffy growth parameters by fitting a linear model to the log-transformed coefficients (k , L_∞ and L_0) of 10 carcharhinid shark populations (Carlson & Baremore 2003, 2005; Carlson, Cortés & Bethea 2003; Lombardi-Carlson *et al.* 2003; Neer, Thompson & Carlson 2005; Carlson, Sulikowski & Baremore 2006; Carlson, Middlemiss & Neer 2007; Piercy *et al.* 2007; Piercy, Carlson & Passerotti 2010). We used these fitted models to provide a continuous range of k , L_∞ and L_0 values (see Table S1). We calculated bias in the estimation of growth coefficient k for this range of life histories as previously; by systematically fixing assumed L_0 as a proportion of real L_0 (over the range from 0.7–1.3). Given that we were not estimating uncertainty, we only drew 1000 k values from each growth model fitted.

Results

COMPARISON OF OBSERVED SIZE AT BIRTH AND ESTIMATED L_0

The ratio between empirical size at birth of elasmobranchs and estimated L_0 from published growth curves ranged between 0.5 and 4.11, but with all ranges falling between 0.7 and 1.3 (Fig. 2, see Table S2). While the two are correlated, only just over half of species (18 of 30) had overlapping size at birth values and L_0 estimates (Fig. 2a). There were no clear patterns or biases in either parameter and no apparent correlation between growth coefficient k and the ratio of size at birth to L_0 estimates (Fig. 2b).

FIXING L_0 OFTEN RESULTS IN BIASED GROWTH ESTIMATES

The growth coefficient (k) estimated using the two-parameter model was increasingly biased as a result of the discrepancy between the actual and assumed L_0 . This bias increased at a rate of approximately a 2.7% change in growth rate (k) for every per cent bias in assumed L_0 . The growth coefficients of both models

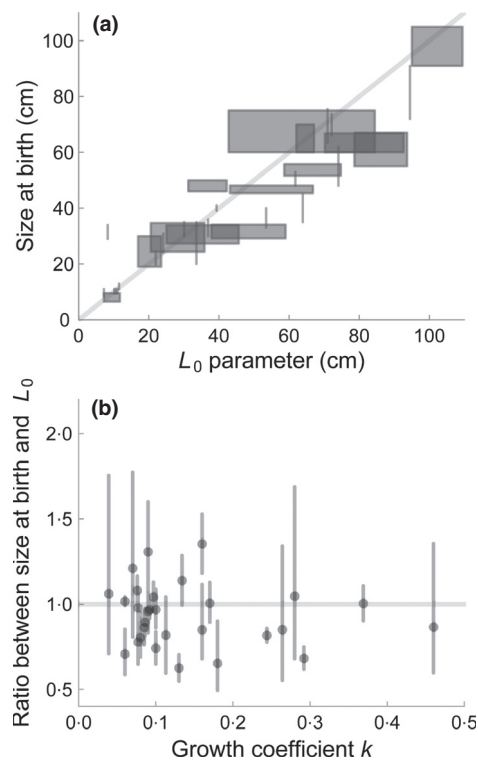


Fig 2. The L_0 parameter of the von Bertalanffy growth equation is not the same as the observed size at birth. (a) Discrepancy between observed sizes at birth and estimated L_0 parameter for 30 elasmobranch species for 41 studies published in the literature. Box width and height represent range in size at birth and variation in L_0 amongst published studies on the same species respectively. Diagonal line indicates 1:1 relationship. (b) Discrepancy between size at birth and L_0 does not vary systematically across life histories, as indexed by growth coefficient k . The ratio for *Deania calcea* lies off the plot and is not included in the graph.

were significantly different (i.e. the 95% quantiles of growth coefficient estimates stopped overlapping) from the true value of k after an approximately 12% discrepancy between the assumed and real L_0 . Fixing L_0 with a smaller than true size at birth resulted in an overestimated growth rate, and *vice versa*. Uncertainty in the growth estimate was comparable when both two- and three-parameter growth models were fit to a large number of data points spanning the complete lifespan of the species (as described by the width of 95% confidence interval; (Fig. 3a).

Uncertainty in the estimate of the growth coefficient (k) was greater for both models when fewer length-at-age data were available. More importantly, the bias of the two-parameter model increased slightly from 2.7% for every per cent change in assumed L_0 in the data-rich scenario (Fig. 3a) to approximately 3% in the thinned scenario (Fig. 3b). In the thinned/no-juveniles scenario, uncertainty in the estimation of k was lower in the two-parameter model, while being extremely high in the three-parameter von Bertalanffy growth function (Fig. 3c). The rate at which k deviates from its true value as L_0

is systematically biased was also slightly reduced in this scenario, with approximately 2% change in k for every per cent change in assumed L_0 .

The degree of bias in growth estimates was greatest for species with slow growth ($k \approx 0.1 \text{ yr}^{-1}$); however, bias was reduced when no data were available in the youngest age classes (note the increased space between isopleths in Fig. 3f compared with Fig. 3d and 3e). In the data-rich scenario, any given discrepancy in L_0 bias was almost twice as high for slow growing species ($k \approx 0.1 \text{ yr}^{-1}$) compared with faster growing species ($k \approx 0.5 \text{ yr}^{-1}$; Fig. 3d). Bias in growth rate estimation decreased considerably as growth coefficient k approached 0.25 yr^{-1} , whereupon it levelled off and remained fairly constant for higher growth rates. The bias in k estimates across a range of life histories in the thinned scenario was similar to the bias in the data-rich scenario, albeit at a slightly higher rate (Fig. 3e). Similar to the previous scenarios, the thinned/no-juveniles scenario produced higher uncertainty in the slowest growing species than in the faster growing ones. Nonetheless, in

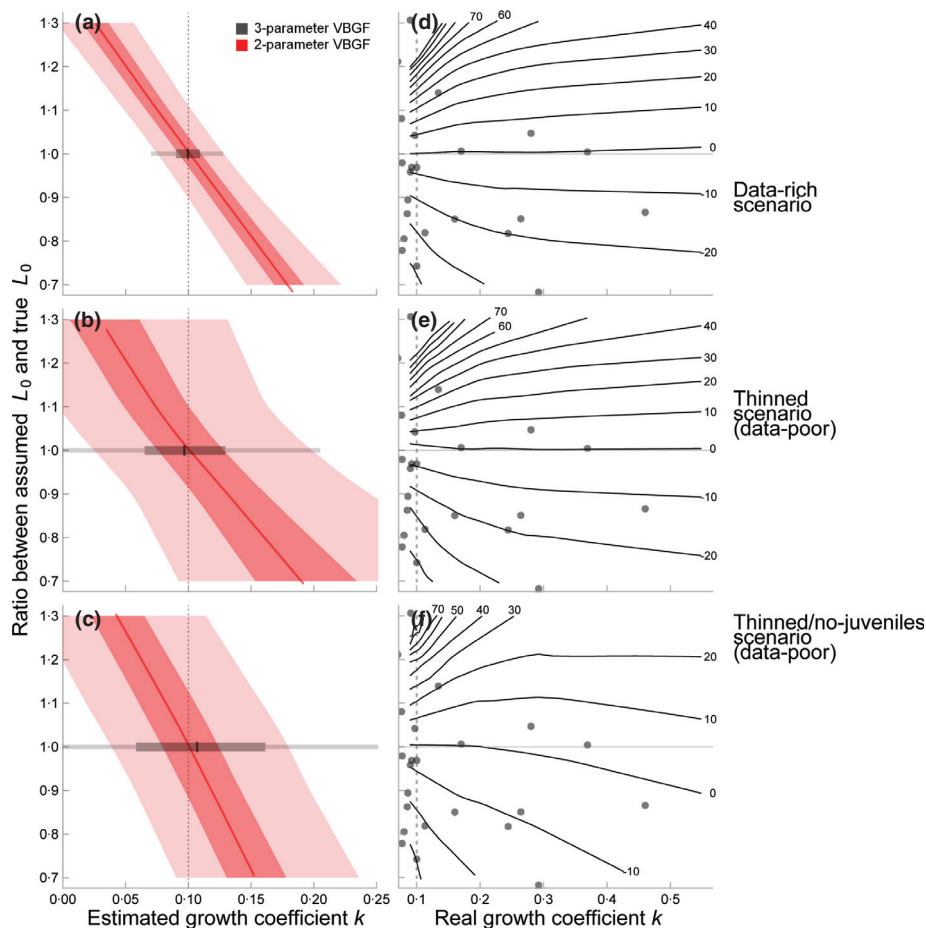


Fig 3. Biased growth estimates from the two-parameter von Bertalanffy growth model for (a, d) data-rich scenario with 150 lengths at each age across all age classes; (b, e) data-poor ('thinned') scenario with 20 lengths at each age across all age classes; and (c, f) 'thinned/no-juveniles scenario' with 20 lengths at each age, but none from the youngest three (0–2 years) age classes. The left-hand panels (a, b, c) show the bias in estimated growth coefficient k across a range of assumed L_0 for a blacknose shark *Carcharhinus acronotus* life history ($L_\infty = 200 \text{ cm}$, $k = 0.1 \text{ yr}^{-1}$, $L_0 = 59.06 \text{ cm}$). Dark lines are the median estimate of k , with 50% (darker shading) and 95% (lighter shading) quantiles for the two- (red) and three- (grey) model. The right-hand column (d, e, f) shows the median bias in estimated k (as a percentage difference from real k) across a fuller range of life histories (x-axis) for varying bias in L_0 (y-axis). Grey dots represent the mean ratios of size at birth to L_0 published in the literature (see Table 1 and Fig. 2b). The dotted lines represent the k value at which (a), (b) and (c) were respectively computed ($k = 0.1 \text{ yr}^{-1}$). All lines are lowess-smoothed.

fast growing species there was a positive bias in the estimation of k even when there was no bias in the assumed L_0 (Fig. 3f).

The range of observed discrepancies between empirical sizes at birth and L_0 (0.62–3.63, see Table S2) was larger than the range of variability in assumed L_0 values used for the simulation models in this study (0.7–1.3, Fig. 3d, e, f). Thus, there is scope for even larger biasing of growth estimates than those explored in this analysis if those extremely dissimilar values of size at birth were used to fix L_0 in the von Bertalanffy growth model.

Discussion

Fixing model parameters may seem like an appealing approach, particularly when faced with few data and one degree of freedom can be saved in the estimation of parameters. However, in the case of the von Bertalanffy growth model, we show how fixing one parameter results in a substantial risk of estimating a biased growth parameter, which far outweighs any benefits of this approach. The modified two-parameter von Bertalanffy growth model does not reduce bias in growth estimates, at least in a scenario with robust length-at-age data, and in fact can potentially increase bias if the value of L_0 is even marginally different from the underlying ‘true’ value. Furthermore, in all scenarios we explored except the thinned/no-juveniles scenario, there was no added benefit of fitting a two-parameter von Bertalanffy growth model to the data.

The findings in this study are also applicable to bony fishes (teleosts) where the t_0 parameterisation of the von Bertalanffy is used, with some studies advocating for fixing the t_0 parameter to zero in particular cases (McGarvey & Fowler 2002; Taylor, Walters & Martell 2005; Gwinn, Allen & Rogers 2010). Given that the t_0 and the L_0 parameterisations are mathematically equivalent (Cailliet *et al.* 2006), fixing it to a specified value will result in the same mathematical constraints and hence similar effects on model performance as those highlighted in our study.

COMPARISON OF OBSERVED SIZE AT BIRTH AND ESTIMATED L_0

The L_0 parameter from the von Bertalanffy growth model is not equivalent to the size at birth observed empirically. This can be due to at least three factors. First, in their birth year, individuals span a range of sizes as a result of differing birth size and foraging competency in the face of predation risk at a time when the gain in weight per gram of individual is greatest. Second, while age should be a continuous variable, it is usually binned in yearly groups due to the practical constraints of age determination. Third, size at birth usually represents the minimum size at which a species is born, and is derived from comparisons between neonates with umbilical scars and fully developed embryos. The suggestion by Cailliet *et al.* (2006) to use all known values of size at birth for a species is not likely to reduce bias in the estimation of growth, as suggested by the similar performance of both two-parameter models tested. We do support their suggestion of comparing the estimated

L_0 parameter from the traditional three-parameter von Bertalanffy growth model with published accounts of size at birth to evaluate how reasonably the model fits the data, in the same way the estimated L_∞ is compared with maximum published size of a given species to assess goodness-of-fit. As pointed out by Knight (1968), the problem lies when parameters from the von Bertalanffy growth model are regarded ‘as a fact of nature rather than as a mathematical artefact of the data analysis’.

THE FUTURE OF THE TWO-PARAMETER VON BERTALANFFY GROWTH MODEL

So, when might we consider using a two-parameter von Bertalanffy growth model instead of the three-parameter variant? Under typical sampling strategies (shown in Fig. 3a,b), the two-parameter von Bertalanffy growth model provides little reduction in uncertainty and risks biasing the estimates of the growth coefficient k . When data are sparse and the sample is mainly comprised of adults (i.e. with few juveniles and sub-adults available) the L_0 parameter will be poorly estimated and, due to the correlation in parameters, will result in a poorly fit model with broad confidence intervals. While bias may be reduced, uncertainty is not vastly improved by using the two-parameter von Bertalanffy growth model. In such a data-poor situation with predominantly adult samples, fixing the L_0 parameter might be justified. However, we warn that even if L_0 is estimated correctly, a sample size of 20 length-at-age points with no juveniles (ages 0–3) results in an estimate of k which has confidence intervals that encompass a $\pm 75\%$ difference from the true value (Fig. 3c, 95% confidence intervals in red). If such a growth curve is fit, it must be recognised that the uncertainty in growth coefficient estimates must be accounted for and propagated in any stock assessments. A novel approach to improving estimation of growth in data-sparse situations with the aid of a known, empirical size at birth, but without using a two-parameter von Bertalanffy growth function, has been outlined by Smart *et al.* (in press) based on back-calculation techniques and has been shown to perform well from an information-theoretic perspective. Testing the performance of this approach under uncertain L_0 parameter values should be the focus of further investigation.

ACCURACY VS. PARSIMONY IN MODEL FITTING

The AIC approach, commonly used in age and growth studies, balances model complexity (number of parameters) and goodness-of-fit (the likelihood), but does not necessarily provide the most unbiased parameter estimates. Previous work has shown that the two-parameter von Bertalanffy growth model was selected most often by AIC (partially because it estimates one less parameter) while at the same time providing the least accuracy in parameter recovery (Thorson & Simpfendorfer 2009). In their study, the fixed L_0 in the two-parameter models equalled true L_0 (i.e. the value of L_0 used to create simulated data points). This scenario is rarely encountered: size at birth is not the same as L_0 (Fig. 2). As we show here, once

uncertainty in size at birth is accounted for, the performance of two-parameter von Bertalanffy model is more biased than originally suspected (Thorson & Simpfendorfer 2009). While AIC can be useful for discriminating between models it does not necessarily provide unbiased parameter estimates, which is the key finding of our study.

CONSEQUENCES FOR FISHERIES ASSESSMENT AND MARINE CONSERVATION

'It ain't what you don't know that gets you into trouble. It's what you know for sure that just ain't so.'

Mark Twain

These findings have important implications for fisheries management and the conservation of marine resources. The growth coefficient k is a key parameter for the estimation of biomass and as such any stock assessment that calculates spawning stock biomass can potentially be profoundly affected by inaccurate estimates of growth. The impact on stock assessments can be explored using a simple yield-per-recruit model (See Appendix 2). An 8% overestimate of L_0 results in a k estimate of 0.08 yr^{-1} (Fig. 3a), which is 20% lower than true k . This in turn leads to a 20.1% reduction in the estimate of yield-per-recruit biomass at $F_{0.1}$ when compared with calculations based on true L_0 . Whereas an 8% underestimate in L_0 causes an overestimation of k of 20% (0.12 yr^{-1}), resulting in a $F_{0.1}$ yield-per-recruit estimate that is 20.8% higher than if true L_0 was used in the estimation of k .

Many life-history invariant relationships are also derived from von Bertalanffy growth parameters (Charnov 1993, 2008; Charnov, Gislason & Pope, in press). In turn, population assessment models, particularly those for data-poor species, make routine use of invariants (Dulvy *et al.* 2004; Le Quesne & Jennings 2012; Pardo, Cooper & Dulvy 2012). For example, a natural mortality parameter is commonly calculated in stock assessments using von Bertalanffy growth parameters as proxies (Pauly 1980; Charnov, Gislason & Pope, in press). Hence, using biased estimates of natural mortality derived from biased estimates of growth can lead to erroneous assessments of stock status. Furthermore, given that von Bertalanffy growth parameters are correlated with each other (Pilling, Kirkwood & Walker 2002), biases in the estimation of growth coefficient (k) will have impacts on the estimation of asymptotic size (L_∞); these parameters covary negatively. Thus, fixing L_0 with a smaller than true value will result in an underestimate of asymptotic size as well as an overestimate of k , which can further affect their effective use as proxies in life-history estimation and stock assessments.

In conclusion, we strongly discourage the use of empirical size at birth for fixing the L_0 parameter in the von Bertalanffy growth model. Furthermore, where multiple growth models are fit and multi-model averaging framework used, these two-parameter model variants should not be considered in the candidate model set unless data are sparse for juvenile age classes. More generally, our case study cautions

against fixing parameters to save a degree of freedom and lower the AIC score of a model without an understanding of the biases that may arise.

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References

- Arntzen, J.W. (2000) A growth curve for the newt *Triturus cristatus*. *Journal of Herpetology*, **34**, 227–232.
- Austin, S.H., Robinson, T.R., Robinson, W.D. & Ricklefs, R.E. (2011) Potential biases in estimating the rate parameter of sigmoid growth functions. *Methods in Ecology and Evolution*, **2**, 43–51.
- Beddington, J.R. & Kirkwood, G.P. (2005) The estimation of potential yield and stock status using life-history parameters. *Philosophical Transactions of the Royal Society B*, **360**, 163–170.
- von Bertalanffy, L. (1938) A quantitative theory of organic growth (inquiries on growth laws, II). *Human Biology, A Record of Research*, **10**, 181–218.
- von Bertalanffy, L. (1957) Quantitative laws in metabolism and growth. *The Quarterly Review of Biology*, **32**, 217–231.
- Beverton, R.J.H. & Holt, S.J. (1959) A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. *Ciba Foundation Colloquia on Ageing* (eds G.E.W. Wolstenholme & M. O'Connor), pp. 142–180. Little, Brown and Company, Boston.
- Braccini, J.M., Gillanders, B.M., Walker, T.I. & Tovar-Avila, J. (2007) Comparison of deterministic growth models fitted to length-at-age data of the piked spurdog (*Squalus megalops*) in south-eastern Australia. *Marine and Freshwater Research*, **58**, 24–33.
- Cailliet, G.M., Smith, W.D., Mollet, H.F. & Goldman, K.J. (2006) Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes*, **77**, 211–228.
- Carlson, J.K. & Baremore, I.E. (2003) Changes in biological parameters of Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the Gulf of Mexico: evidence for density-dependent growth and maturity? *Marine and Freshwater Research*, **54**, 227–234.
- Carlson, J.K. & Baremore, I.E. (2005) Growth dynamics of the spinner shark (*Carcharhinus brevipinna*) off the United States southeast and Gulf of Mexico coasts: a comparison of methods. *Fishery Bulletin*, **103**, 280–291.
- Carlson, J.K., Cortés, E. & Bethea, D.M. (2003) Life history and population dynamics of the finetooth shark (*Carcharhinus isodon*) in the northeastern Gulf of Mexico. *Fishery Bulletin*, **101**, 281–292.
- Carlson, J.K., Middlemiss, A.M. & Neer, J.A. (2007) A revised age and growth model for blacknose shark, *Carcharhinus acronotus* from the eastern Gulf of Mexico using X-radiography. *Gulf of Mexico Science*, **25**, 82–87.
- Carlson, J.K., Sulikowski, J.R. & Baremore, I.E. (2006) Do differences in life history exist for blacktip sharks, *Carcharhinus limbatus*, from the United States South Atlantic Bight and Eastern Gulf of Mexico? *Environmental Biology of Fishes*, **77**, 279–292.
- Charnov, E.L. (1993) *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford University Press, Oxford.
- Charnov, E.L. (2008) Fish growth: Bertalanffy k is proportional to reproductive effort. *Environmental Biology of Fishes*, **83**, 185–187.
- Charnov, E.L., Gislason, H. & Pope, J.G. (in press) Evolutionary assembly rules for fish life histories. *Fish and Fisheries*. <http://dx.doi.org/10.1111/j.1467-2979.2012.00467.x> [accessed 20 June 2012]
- Chen, Y., Jackson, D.A. & Harvey, H.H. (1992) A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 1228–1235.
- Compagno, L.J.V. (1984a) Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. *FAO Fisheries Synopsis*, **125**, 1–249.
- Compagno, L.J.V. (1984b) Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. *FAO Fisheries Synopsis*, **125**, 251–655.

- Dulvy, N.K., Ellis, J.R., Goodwin, N.B., Grant, A., Reynolds, J.D. & Jennings, S. (2004) Methods of assessing extinction risk in marine fishes. *Fish and Fisheries*, **5**, 255–276.
- Einum, S., Forseth, T. & Finstad, A.G. (2012) Individual variation in response to intraspecific competition: problems with inference from growth variation measures. *Methods in Ecology and Evolution*, **3**, 438–444.
- English, S., Bateman, A.W. & Clutton-Brock, T.H. (2012) Lifetime growth in wild meerkats: incorporating life history and environmental factors into a standard growth model. *Oecologia*, **169**, 143–153.
- Fabens, A.J. (1965) Properties and fitting of the von Bertalanffy growth curve. *Growth*, **29**, 265–289.
- Frisk, M.G., Miller, T.J. & Dulvy, N.K. (2005) Life histories and vulnerability to exploitation of elasmobranchs: inferences from elasticity, perturbation and phylogenetic analyses. *Journal of Northwest Atlantic Fishery Science*, **37**, 27–45.
- Frisk, M.G., Miller, T.J. & Fogarty, M.J. (2001) Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 969–981.
- Gwinn, D.C., Allen, M.S. & Rogers, M.W. (2010) Evaluation of procedures to reduce bias in fish growth parameter estimates resulting from size-selective sampling. *Fisheries Research*, **105**, 75–79.
- Hilborn, R. & Mangel, M. (1997) *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton.
- Hoenig, J.M. (1983) Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin*, **82**, 898–903.
- Jennings, S., Reynolds, J.D. & Mills, S.C. (1998) Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society B*, **265**, 333–339.
- Katsanevakis, S. (2006) Modelling fish growth: model selection, multi-model inference and model selection uncertainty. *Fisheries Research*, **81**, 229–235.
- Katsanevakis, S. & Maravelias, C.D. (2008) Modelling fish growth: multi-model inference as a better alternative to a priori using von Bertalanffy equation. *Fish and Fisheries*, **9**, 178–187.
- Knight, W. (1968) Asymptotic growth: an example of nonsense disguised as mathematics. *Journal of the Fisheries Research Board of Canada*, **25**, 1303–1307.
- Le Quesne, W.J.F. & Jennings, S. (2012) Predicting species vulnerability with minimal data to support rapid risk assessment of fishing impacts on biodiversity. *Journal of Applied Ecology*, **49**, 20–28.
- Lehman, T.M. & Woodward, H.N. (2008) Modeling growth rates for sauropod dinosaurs. *Paleobiology*, **34**, 264–281.
- Lester, N.P., Shuter, B.J. & Abrams, P.A. (2004) Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society B*, **271**, 1625–1631.
- Lombardi-Carlson, L.A., Cortés, E., Parsons, G.R. & Manire, C.A. (2003) Latitudinal variation in life-history traits of bonnethead sharks, *Sphyrna tiburo* (Carcharhiniformes: Sphyrnidae) from the eastern Gulf of Mexico. *Marine and Freshwater Research*, **54**, 875–883.
- McGarvey, R. & Fowler, A.J. (2002) Seasonal growth of King George whiting (*Sillaginodes punctata*) estimated from length-at-age samples of the legal-size harvest. *Fishery Bulletin*, **100**, 545–558.
- Neer, J.A., Thompson, B.A. & Carlson, J.K. (2005) Age and growth of *Carcharhinus leucas* in the northern Gulf of Mexico: incorporating variability in size at birth. *Journal of Fish Biology*, **67**, 370–383.
- Paine, C.E.T., Matthews, T.R., Vogt, D.R., Purves, D., Rees, M., Hector, A. & Turnbull, L.A. (2012) How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. *Methods in Ecology and Evolution*, **3**, 245–256.
- Pardo, S.A., Cooper, A.B. & Dulvy, N.K. (2012) Critical review and analysis of existing risk-based techniques for determining sustainable mortality levels of bycatch species. DFO Canadian Science Advisory Secretariat. Research Document 2012/014. iv + 30 p.
- Pauly, D. (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer*, **39**, 175–192.
- Pierce, S.J. & Bennett, M.B. (2010) Destined to decline? Intrinsic susceptibility of the threatened estuary stingray to anthropogenic impacts. *Marine and Freshwater Research*, **61**, 1468–1481.
- Piercy, A.N., Carlson, J.K. & Passerotti, M.S. (2010) Age and growth of the great hammerhead shark, *Sphyrna mokarran*, in the north-western Atlantic Ocean and Gulf of Mexico. *Marine and Freshwater Research*, **61**, 992–998.
- Piercy, A.N., Carlson, J.K., Sulikowski, J.A. & Burgess, G.H. (2007) Age and growth of the scalloped hammerhead shark, *Sphyrna lewini*, in the north-west Atlantic Ocean and Gulf of Mexico. *Marine and Freshwater Research*, **58**, 34–40.
- Pilling, G.M., Kirkwood, G.P. & Walker, S.G. (2002) An improved method for estimating individual growth variability in fish, and the correlation between von Bertalanffy growth parameters. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 424–432.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. URL <http://www.r-project.org/> [accessed 29 February 2012]
- Smart, J.J., Harry, A.V., Tobin, A.J. & Simpfendorfer, C.A. (in press) Overcoming the constraints of low sample sizes to produce age and growth data for rare or threatened sharks. *Aquatic Conservation: Marine and Freshwater Ecosystems*. <http://dx.doi.org/10.1002/aqc.2274> [accessed 13 June 2012].
- Taylor, N.G., Walters, C.J. & Martell, S.J.D. (2005) A new likelihood for simultaneously estimating von Bertalanffy growth parameters, gear selectivity, and natural and fishing mortality. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 215–223.
- Thorson, J.T. & Simpfendorfer, C.A. (2009) Gear selectivity and sample size effects on growth curve selection in shark age and growth studies. *Fisheries Research*, **98**, 75–84.
- Tjørvæ, K.M.C. & Tjørvæ, E. (2010) Shapes and functions of bird-growth models: how to characterise chick postnatal growth. *Zoology*, **113**, 326–333.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. R code for fitting three- and two-parameter von Bertalanffy growth functions (VBGF) using the nls() function.

Appendix S2. R code for assessing the effect of slight variations in growth coefficient (k) estimates on a simple yield-per-recruit model of *Carcharhinus brevipinna*.

Table S1. Range of von Bertalanffy growth parameter values (L_{∞} , k , and L_0) used for the estimation of bias from fixing L_0 through a life history continuum. Life histories were modeled based on carcharhinid and sphyrnid sharks. Table is ordered from high to low k values with the table split into two columns.

Table S2. Data used for calculating empirical discrepancies between size at birth and the L_0 parameter from the von Bertalanffy growth function. Species are ordered taxonomically. FL = fork length, TL = total length, PCL = precaudal length, and DW = disc width. References used in the table are listed below.