

# Two Bayesian methods for estimating parameters of the von Bertalanffy growth equation

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**Abstract** The von Bertalanffy growth equation (VBGE) is commonly used in ecology and fisheries management to model individual growth of an organism. Generally, a nonlinear regression is used with length-at-age data to recover key life history parameters:  $L_{\infty}$  (asymptotic size),  $k$  (the growth coefficient), and  $t_0$  (a time used to calculate size at age 0). However, age data are often unavailable for many species of interest, which makes the regression impossible. To confront this problem, we have developed a Bayesian model to find  $L_{\infty}$  using only length data. We use length-at-age data for female blue shark, *Prionace glauca*, to test our hypothesis. Preliminary comparisons of the model output and the results of a nonlinear regression using the

VBGE show similar estimates of  $L_{\infty}$ . We also developed a full Bayesian model that fits the VBGE to the same data used in the classical regression and the length-based Bayesian model. Classical regression methods are highly sensitive to missing data points, and our analysis shows that fitting the VBGE in a Bayesian framework is more robust. We investigate the assumptions made with the traditional curve fitting methods, and argue that either the full Bayesian or the length-based Bayesian models are preferable to classical nonlinear regressions. These methods clarify and address assumptions made in classical regressions using von Bertalanffy growth and facilitate more detailed stock assessments of species for which data are sparse.

**Keywords** Markov Chain Monte Carlo · Elasmobranch · Stock assessment · Asymptotic size

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## Introduction

The von Bertalanffy growth equation (VBGE) can be used to describe the way individual organisms grow (von Bertalanffy 1938, 1957). The form used by Beverton and Holt (1959) is the following

$$L(a) = L_{\infty} \left( 1 - e^{-k(a-t_0)} \right) \quad (1)$$

where  $a$  is age,  $k$  is the growth coefficient,  $t_0$  is a value used to calculate size when age is zero, and  $L_{\infty}$  is asymptotic size. Generally, to obtain estimates of the parameters, the VBGE is fit to length-at-age data using classical nonlinear regression techniques (Grafen and Hails 2002). This curve-fitting technique somewhat changes the assumptions of the VBGE; using a least squares estimate assumes an average maximum size for the population rather than a truly asymptotic size—often termed  $L_{\max}$  in the literature rather than  $L_{\infty}$ . However, there is a physiological maximum size a fish can attain. Bayesian methods presented in this paper allow for the use of the VBGE while maintaining its biological assumptions.

Individual growth is the basis of many stock assessment models (Jennings et al. 2001). However, length-at-age data—required for parameter estimation—are not available or abundant for many populations, particularly for long-lived species. Length data are easier to gather, and more available for fished species. We developed a Bayesian model to estimate the maximum size using only length data.

We also present a full Bayesian model designed to fit the VBGE to the length-at-age data. We include literature-derived priors in our analysis and compare our results from both Bayesian models to the results from a classical nonlinear regression.

## Methods

We have length-at-age data with  $a = 0, \dots, i$  indexing age and  $r$  indexing the number of length data per age. The number of data varies per age, and the following is a visualization of our data:

$$\begin{array}{cccc} a = 1 & L_{1,1} & \dots & L_{1,r} \\ \vdots & \vdots & & \vdots \\ a = i & L_{i,1} & \dots & L_{i,r} \end{array} \quad (2)$$

There are likely two sources of error in our data: process error and observation error (Hilborn and Mangel 1997). We expect the process error to be the variability of vital rates such as growth and mortality within each age class. Observation error will manifest in the way each population is sampled; we expect to see variation in the selectivity of the gear (i.e. the distribution of sizes caught by the gear type). However, for this paper, we include one multiplicative error term to represent all error.

For each of the following models, we used the same data set from the literature to test the ideas (Acuña et al. 2001).<sup>1</sup> The length-at-age data are for female blue shark, *Prionace glauca*, from the Eastern Tropical Pacific, representing ages 0–14. We used only female shark data, since many shark species have different growth trajectories for each sex (Cortés 2000). Although we have length-at-age data, we only use the age data for the least squares regression and the full Bayesian model.

### Least squares regression

Least squares regression is a common technique used to fit curves to data (Grafen and Hails 2002). We used the VBGE (Eq. 1) to calculate predicted length at age and then compared those values with the observed length data. The best fit parameters minimize the sum of the squared differences between predicted and observed lengths. For this analysis, we used the solver in Microsoft Excel to find the best combination of parameters minimize the sum of the squared errors.

### Full Bayesian model

Our full Bayesian model fits the VBGE to the length-at-age data using Markov Chain Monte Carlo (MCMC) methods (Hastings 1970; Gelman et al. 2004). These methods require the following four steps:

- (1) Find the likelihood of the data,
- (2) Establish priors for all parameters,

<sup>1</sup> See the reference for sampling and aging methods.

- (3) Find the full conditional probabilities for parameters, when possible, and
- (4) Decide whether to use the Metropolis Hastings or the Gibbs sampling algorithm to sample the posterior distribution for each parameter (Gelman et al. 2004).

We start with the VBGE, including multiplicative error

$$L(a) = L_{\infty} \left(1 - e^{-k(a-t_0)}\right) e^{\varepsilon_a} \quad (3)$$

and then find the log transform

$$l_a = l_{\infty} + \log \left(1 - e^{-k(a-t_0)}\right) + \varepsilon_a \quad (4)$$

$$\varepsilon_a \sim N(0, \sigma^2) \quad (5)$$

where the lower case  $l$  indicates the log of the value. Thus, our likelihood is the following:

$$L(l_{ar}|l_{\infty}, k, t_0, \sigma^2) \propto \prod_{a=0}^{14} \prod_{r=1}^{R_a} \frac{1}{\sqrt{2\pi\sigma^2}} \exp \left\{ -\frac{1}{2\sigma^2} (l_{ar} - (l_{\infty} + \log(1 - \exp\{-k(a-t_0)\})))^2 \right\} \quad (6)$$

where  $R_a$  is the number of length data for each age.

We constructed informative priors for  $k$  and  $t_0$  based on published estimates of the same parameters in the literature for blue shark (Holden 1973; Cailliet et al. 1983; Hoenig and Gruber 1990; Cortés 2000):

$$p(k) = \text{Gamma}(15, 100)^2 \quad (7)$$

$$p(-t_0) = \text{Gamma}(14, 4) \quad (8)$$

We show the probability density functions (pdfs) of the priors for  $k$  and  $t_0$  in Figs. 1 and 2 respectively. We used diffuse priors for  $l_{\infty}$  and  $\sigma^2$ , giving the full power of estimation to the data:

$$p(l_{\infty}) \propto 1 \quad (9)$$

<sup>2</sup> We used the following form of the gamma distribution:  $\text{Gamma}(\alpha, \beta) \sim \frac{\beta^{\alpha}}{\Gamma(\alpha)} x^{\alpha-1} e^{-x\beta}$  for  $x > 0$

$$p(\sigma^2) \propto \frac{1}{\sigma^2} \quad (10)$$

Our prior for  $\sigma^2$  is a Jeffreys prior (a form of non-informative prior, see Gelman et al. 2004). Marginalizing the joint posterior—the likelihood multiplied by the four priors—for each parameter gave two full conditionals:<sup>3</sup>

$$L_{\infty} \sim \text{log normal} \left( \bar{l} - \frac{\sum_{a=0}^{14} \sum_{r=1}^{R_a} \log(1 - \exp\{-k(a-t_0)\})}{n}, \frac{\sigma^2}{n} \right) \quad (11)$$

$$\sigma^2 \sim \text{Inverse-gamma} \left( \frac{n}{2}, 2 \sum_{a=0}^{14} \sum_{r=1}^{R_a} \left( l_{ar} - \left( l_{\infty} + \log(1 - \exp\{-k(a-t_0)\}) \right) \right)^2 \right) \quad (12)$$

where  $\bar{l}$  is the average logged lengths and  $R_a$  is the number of lengths for each age (Appendix).

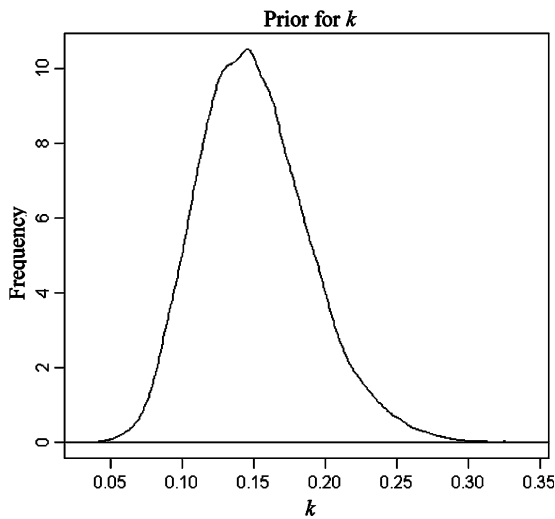
Since the conditional probabilities for  $l_{\infty}$  and  $\sigma^2$  are known pdfs (Eqs. 9 and 10), we used a Gibbs sampler for these parameters in the MCMC. However, we had to use a Metropolis step for  $k$  and  $t_0$  because we could not find their full conditional distributions. We used a random walk jumping distribution<sup>4</sup> for both Metropolis steps.

## Length-based Bayesian model

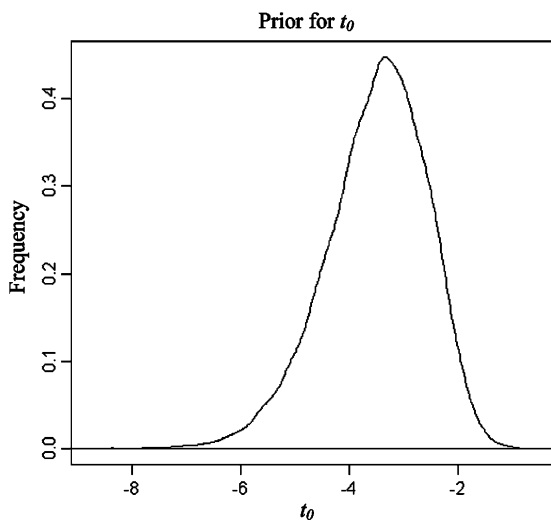
The full Bayesian model is not only computationally intensive but also requires length-at-age data. For cases where only length data are available—which is frequently the case in developing fisheries—we developed a method to estimate the maximum size of the fish in the stock using the

<sup>3</sup> For the functional forms of the lognormal or inverse-gamma distributions, see Gelman et al. (2004)

<sup>4</sup> A random walk jumping distribution samples the probability space around the initial point following a normal distribution, with the initial point as the mean of the normal. The variance is subjectively changed at the start of each MCMC run to achieve a desirable acceptance rate, between 0.3 and 0.5. See Hastings (1970)



**Fig. 1** The frequency of values for  $k$ , the Brody growth coefficient, given the prior probability density. Most of the density lies between 0.09 and 0.19

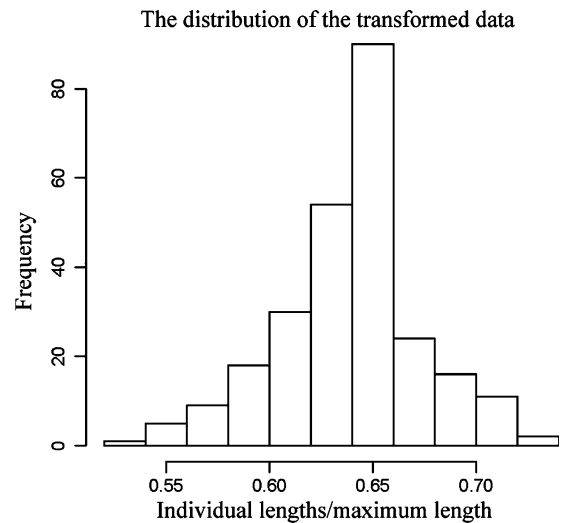


**Fig. 2** The frequency of values for  $t_0$  given the prior probabilities. Most of the density lies between  $-2$  and  $-5$

available data. The new method employs the following Bayesian model. Let  $\{x_1, \dots, x_n\}$  be individual lengths and

$$Y_i = \log \left( \frac{x_i}{1 - \frac{x_i}{\theta}} \right) \quad \text{for } x_i < \theta \quad (13)$$

where  $\theta$  is our proxy for  $L_{\max}$  and we assume  $Y_i \sim N(\mu, \sigma^2)$ . A plot of the transformed data was used to determine if the  $Y_i$ s were distributed



**Fig. 3** A histogram of the transformed data shows an approximate normal distribution

normally (Fig. 3). We used the logit transformation of the individual lengths divided by the maximum datum. The parameter  $\theta$  is our proxy to the maximum attainable size a fish in the population can achieve. Our key condition is that all data be less than  $\theta$ .

Our likelihood is the following, based on the normal distribution of the  $Y_i$ s:

$$L(\mu, \sigma^2, \theta) = \exp \left\{ \frac{1}{2\sigma^2} \sum_{i=1}^n \left( \log \left( \frac{x_i}{1 - \frac{x_i}{\theta}} \right) - \mu \right)^2 \right\} \left( \frac{1}{\sigma^2} \right)^{\frac{n}{2}} \left( \prod_{i=1}^n \frac{1}{x_i (1 - \frac{x_i}{\theta})} \right) \quad (14)$$

We include no information from the literature for the mean and variance parameters of the normal distribution in Eq. 14 by assuming Jeffreys priors for both parameters

$$p(\mu, \sigma^2) \propto \frac{1}{\sigma^2} \quad (15)$$

However, we used information from the literature for our prior for  $L_{\max}(\theta)$

$$p(\theta) \sim \text{Normal}(310, 80) \quad (16)$$

where 310 cm TL is the mean and 80 is the variance of the normal prior. From the full joint posterior, we found two full conditionals

$$p(\mu|\sigma^2, \theta, \text{data}) \propto \text{Normal}\left(\frac{1}{n} \sum_i \left(\frac{x_i}{1 - \frac{x_i}{\theta}}\right), \frac{\sigma^2}{n}\right) \quad (17)$$

$$p(\sigma^2|\mu, \theta, \text{data}) \propto \text{Inverse} - \text{gamma} \left( \frac{n}{2}, \frac{2}{\sum_{i=1}^n \left(\log\left(\frac{x_i}{1 - \frac{x_i}{\theta}}\right) - \mu\right)^2} \right) \quad (18)$$

Again, since we have recognizable pdfs for  $\mu$  and  $\sigma^2$ , we used a Gibbs sampler for these parameters. We used the Metropolis Hastings algorithm with a random walk jumping distribution<sup>3</sup> to find  $\theta$  (Hastings 1970).

## Results

### Least squares method

The combination of parameters that minimized the sum of the squared error was 252 cm, 0.13, and −3.09 for  $L_\infty$ ,  $k$ , and  $t_0$  respectively (Table 1).

### Full Bayesian model

We used a burn-in period of 1,000 samples and generated posteriors for the three parameters of the VBGE with the remaining samples. Our mean results are as follows: 419 cm TL, 0.06, and −3.25 for  $L_\infty$ ,  $k$ , and  $t_0$  respectively. We include 95% probability intervals for each estimate in Table 1.

### Length-based Bayesian model

We initialized the model with a number slightly larger than the maximum data point. The chain converged quickly to an estimate of 308 cm (Table 1). Using our estimate for  $L_\infty$  in the least squares regression, we generated a value for  $k$  and  $t_0$  to use for comparison (0.08 and −4.13 respectively).

### Convergence

We tested the convergence of our Bayesian models using both the Z-scores of the Geweke

test, and by starting the runs at various initial values to see if the sample chains converge on the same number. Both tests were successful, showing convergence in the models.<sup>5</sup>

## Discussion

### Comparing estimates

First, we compare the least squares regression and the full Bayesian model (Figs. 4, 5 & Table 1). The estimates of  $t_0$  are very similar; however, the difference in assumptions is very obvious when comparing the estimates of  $L_\infty$  and  $k$ . The full Bayesian model estimates a much larger asymptote. However, since  $L_\infty$  and  $k$  are inversely proportional, we expect, and find, a much smaller  $k$  estimate.<sup>6</sup> To ensure the difference between the model estimates was not only due to that correlation, we checked the correlation between parameters and the influence of the priors on the estimates (Fig. 6). The scatter plots have no structure in any of the other parameters, therefore we ruled out other correlations. We then examined the sensitivity of the full Bayesian model to the informative prior for  $k$ . Recall the mean of the gamma prior for  $k$  was 0.15. Our full Bayesian model estimate is 0.06, which means that there was enough information in the data to overwhelm any influence of the prior on the estimate (Fig. 7). In fact, when we used a non-informative prior for  $k$ , the posterior estimate was not significantly different. We also removed the ten largest data points and ran the full Bayesian model and classical regression again. The Bayesian model output did not change significantly, but the regression results changed drastically. Therefore, we are confident with our model estimates for the full Bayesian model.

Next, we compare the least squares regression with the length-based Bayesian model. The esti-

<sup>5</sup> See Gelman et al. (2004). For information on convergence diagnostics.

<sup>6</sup> The VBGE comes from the following differential equation:  $\frac{dL}{dt} = k(L_\infty - L)$ . When most of the data are small lengths, it becomes  $\frac{dL}{dt} \approx kL_\infty$  if  $L_\infty \gg L$ , exacerbating the correlation problem.

**Table 1** A summary of the results from the three different models

Model	Estimate of $L_{\infty}$	Estimate of $k$	Estimate of $t_0$
Least squares estimation (VBGE)	252 cm [192, 312]	0.13	−3.09
Full Bayesian model (VBGE)	419 cm [378, 457]	0.06 [0.05, 0.07]	−3.25 [−3.23, −3.29]
Length-based Bayesian model	308 cm [304, 312]	0.08	−4.13

All three parameters are estimated using the two models that use age data. Although our length-based model only estimates  $L_{\infty}$ , it is possible to draw a von Bertalanffy growth curve using the inverse relationship between  $k$  and  $L_{\infty}$ .

mates of these two models overlap significantly (Table 1). In fact, the mean of the length-based model is well within the confidence interval of the regression.

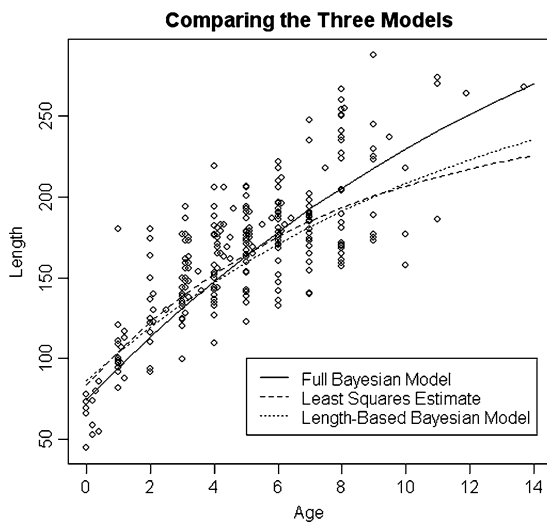
Finally, we compare the two Bayesian models (Table 1). The length-based model is essentially a compromise between the physiological basis of the VBGE and the availability of length-at-age data. It performs similarly to the least squares regression while maintaining the maximum size assumption (recall that the logit treats all data as a proportion relative to the maximum datum). However, we argue that the full Bayesian model is the most desirable model, if the data are available. The maximum reported size of blue shark is 396 cm TL (Smith 2006) and our full Bayesian estimate is closer than the length-based

model estimate. However, when length-at-age data are unavailable, this new method provides a sound estimate of asymptotic size. As data availability and sampling coverage improve, we expect the length-based model estimate to converge on the full Bayesian estimate.

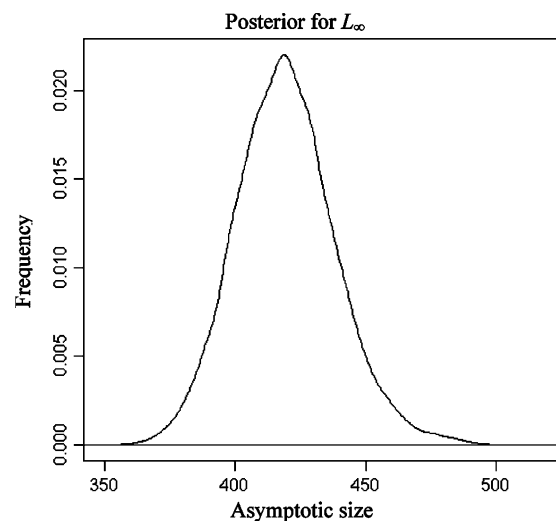
## Conclusion

Our full and length-based Bayesian models are designed to solve two problems: estimate asymptotic size in the absence of length-at-age data, and maintain the biological assumptions of the VBGE when fitting the model to data.

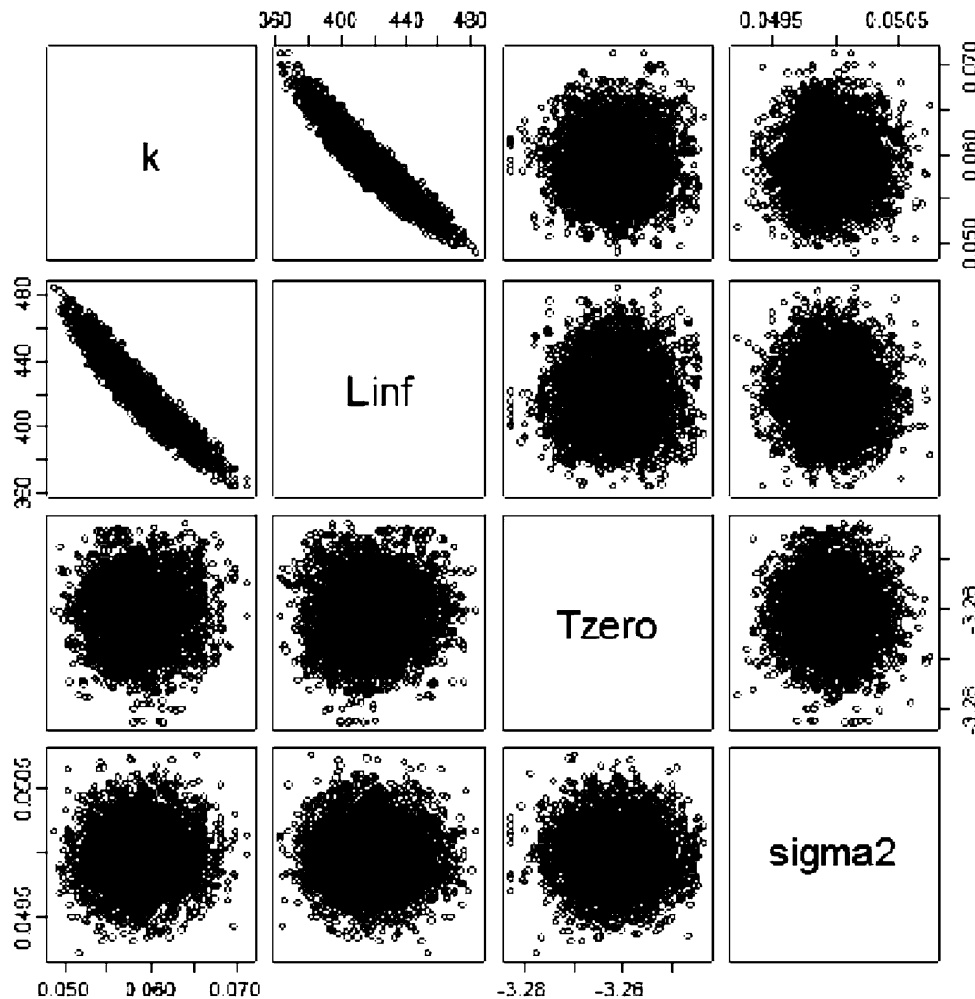
The length-based method uses the distribution of the data to determine what the maximum size is for individuals in the population. In contrast, the least squares regression calculates an average



**Fig. 4** The full Bayesian model and the least squares regression are fit to the length-at-age data for the female blue shark. The Bayesian model assumes  $L_{\infty}$  is a true asymptote



**Fig. 5** The posterior of  $L_{\infty}$  for the full Bayesian model



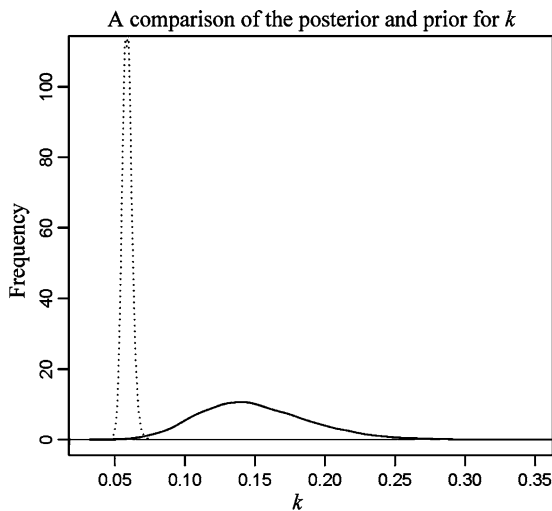
**Fig. 6** This plot illustrates the correlation between each of the estimated parameters. Each row and column is one parameter; in order from top to bottom we plotted  $k$ ,  $L_{\infty}$ ,

$t_0$ , and  $\sigma^2$ . For little or no correlation, we expect a structureless scatterplot. There is an apparent inverse correlation between  $k$  and  $L_{\infty}$ .

maximum size across individuals in the population. The distinction is a subtle, but important one. That is, how should one think about asymptotic size? Is it an individual or population-level parameter? Data are gathered to assess population dynamics, and we offer our length-based and full Bayesian models to assess parameters on the population scale. Our methods are generally applicable to species for which we expect asymptotic growth, and they may be particularly useful for assessments of developing fisheries or of long-lived fishes.

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**Fig. 7** The posterior of  $k$  for the full Bayesian model (dashed line) plotted against its prior (solid line)

## Appendix

### The full Bayesian model

In our computations, we replaced  $t_0$  with  $q$  because it is easier to work with a strictly positive distribution. At the end of the model runs, we take the negative results for  $q$  and set them equal to  $t_0$ .

Our joint posterior is the combination of the four priors—for  $k$ ,  $q$ ,  $L_\infty$ , and  $\sigma^2$ —and the likelihood:

$$p(l_\infty, k, q, \sigma^2 | l_{ar}) \propto \frac{1}{\sigma^2} q^{13} \exp\{-4q\} k^{-85} \\ \exp\{-k(100)\} \times \prod_{a=0}^{15} \prod_{r=1}^R \frac{1}{\sqrt{2\pi\sigma^2}} \\ \exp\left\{-\frac{1}{2\sigma^2}(l_{ar} - (l_\infty + \log(1 - \exp\{-k(a+q)\})))^2\right\}$$

Marginalizing, or multiplying out each of the parameters one at a time, give us either a formula to use in a Metropolis Hastings algorithm or a full conditional to use with a Gibbs sampler as detailed in the main text.

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