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Growing the biphasic framework: Techniques and recommendations for fitting emerging growth models

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Abstract

1. Several new growth models have been proposed to account for the life-history trade-offs that occur when indeterminately growing species allocate energy between somatic growth and reproduction. These models can improve the understanding of lifetime growth and life history, but can be more difficult to fit than conventional growth models. Increased data demands, multiple growth phases and increased parameterization all serve as barriers to the adoption and proper use of these new models.

2. We review and comment on confounding issues during model fitting for several of these models, and provide advice on surmounting such issues. We then simulation-test an example model, the Lester biphasic growth model, using several common fitting approaches. We highlight the biases and precision of each approach and provide guiding documents using R and JAGS code.

3. The Bayesian Markov chain Monte Carlo and likelihood profiling approaches generally provided the best fits. Simpler approaches can be unbiased and precise if sampled data are of relatively high quality (e.g. moderate sample sizes for juvenile and adult phases) and model assumptions are met. Bayesian hierarchical approaches can accommodate more complicated data scenarios (e.g. unbalanced design across multiple populations); we provide an example of such an approach by recovering growth trajectories and inferring growth-associated trait variation and environmental effects across multiple populations.

4. Conventional growth models provide limited inference on life history. Many biphasic growth models can provide direct inference on multiple life-history traits, but can be difficult to fit. The recommended approaches herein provide a path forward for fitting biphasic growth models in a variety of scenarios, allowing for wider application and tests of life history and ecological theory.

KEYWORDS
Bayesian, growth estimation, hierarchical models, life-history theory, likelihood profiling, polyphasic growth, somatic growth

1 | INTRODUCTION

Understanding the rate at which individuals or cohorts grow is a major focus of modern biology. Growth results from a diversity of ecological and evolutionary factors and processes. Growth can therefore be used as an indicator of metabolic rate, nutrition, reproductive investment, behaviour, individual and population health, within- and among-species interactions, habitat and more (Dmitriew, 2011; Dobbertin,
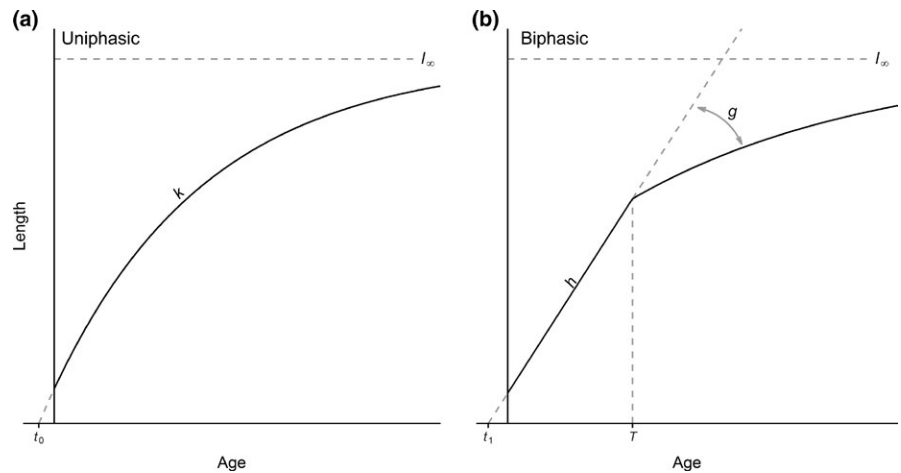
FIGURE 1 Comparison of the (a) uniphasic von Bertalanffy model versus the (b) Lester biphasic model. The Lester model assumes that growth leading up to maturity (h) is linear, and that growth shifts when individuals mature (T) due to energetic investment in reproduction (g). t_0 = von Bertalanffy (adult) hypothetical age at length 0; t_1 = Lester model (immature) hypothetical age at length 0; k = von Bertalanffy (Brody) growth coefficient; l_∞ = asymptotic length

2005; Honsey, Staples, & Venturelli, 2017; Rennie & Venturelli, 2015). Growth and size are also under strong selection (Dmitriew, 2011; Okie et al., 2013), correlated with a suite of life-history traits that are important to fitness and population growth (Roff, 1983; Stearns, 1992), and often central to management and conservation (Lorenzen, 2016).

Most vertebrate and plant studies (Paine et al., 2012) describe lifetime growth as a single curve, but this approach has been criticized. Popular uniphasic models include the logistic, Gompertz and von Bertalanffy models (Pardo, Cooper, & Dulvy, 2013). These curves tend to be straightforward to fit and are usually applied to cross-sectional or longitudinal size-at-age data from single populations. A common criticism of these models, particularly in the fish literature, is that lifetime growth comprises two or more stages that result from reproductive investment (Day & Taylor, 1997; Lester, Shuter, & Abrams, 2004) or changes in habitat, food or other stressors (Paloheimo & Dickie, 1965; Parker & Larkin, 1959; Figure 1). Describing these stages with a single curve can obscure important ecological and evolutionary information.

At least 26 biphasic growth models have been proposed for, or are commonly applied to, fishes (Table 1). These models vary in complexity (Minte-Vera, Maunder, Casselman, & Campana, 2016) and tend to describe either an abrupt or smooth transition between growth phases. Most transitions are associated with reproductive investment, although changes in age, diet and habitat are also cited. The von Bertalanffy model is commonly used for at least one phase. Such an approach is consistent with von Bertalanffy's (1957) contention that different parameter values were needed for juveniles and adults (Boukal, Dieckmann, Enberg, Heino, & Jorgensen, 2014), but inconsistent with the modern convention of fitting this model to entire growth histories (Ogle, 2016).

There are advantages to biphasic growth models, but fitting them can be a challenge. Biphasic models allow for the estimation of more life-history traits from growth data compared to uniphasic models (e.g. age-at-maturity; Honsey et al., 2017), can be more statistically or biologically valid than uniphasic models (Lester et al., 2004; Moe, 2015; Quince, Abrams, Shuter, & Lester, 2008b; Roff, Heibo, & Vøllestad, 2006), can relate to behavioural pace-of-life syndromes (Nakayama, Rapp, & Arlinghaus, 2017), can estimate management reference points

(Lester, Shuter, Venturelli, & Nadeau, 2014) and can provide evolutionary insight (Roff, 1983; Roff et al., 2006). Biphasic models that explicitly account for energetic costs of reproduction (only implicit with uniphasic models) can also test plastic or evolutionary hypotheses when ecosystem changes alter reproductive schedules (Lorenzen, 2016). However, biphasic models can be difficult to fit due to correlations among parameters, increased model complexity and lack of software. For example, parameter correlations from biphasic models are often similar to the uniphasic von Bertalanffy model ($\rho \approx |0.7|$), except with more parameters (Helser & Lai, 2004; Minte-Vera et al., 2016; Mollet, Ernande, Brunel, & Rijnsdorp, 2010). These correlations can lead to errors during estimation (Minte-Vera et al., 2016; Mollet et al., 2010). Although the life-history trade-offs and correlations of many biphasic models can improve ecological inference (e.g. life-history invariants; Shuter et al., 2005), these challenges preclude their straightforward application.

Herein, we present techniques, discuss recommendations and provide companion code in R (R Core Team, 2016) and JAGS (Plummer, 2003) for fitting biphasic growth models across a range of scenarios. We demonstrate these concepts using the Lester biphasic model (LM; Lester et al., 2004), which is popular in the fish literature and has been adapted for a diversity of ecological and evolutionary applications (Enberg, Jørgensen, Dunlop, Heino, & Dieckmann, 2009; Giacomini & Shuter, 2013; Honsey et al., 2017; Johnston, Arlinghaus, & Dieckmann, 2010; Lester et al., 2014; Rennie, Collins, Shuter, Rajotte, & Couture, 2005). Finally, we provide guidance regarding which approaches to use via simulation tests that evaluate bias and precision for a range of statistical approaches.

2 | THE LESTER BIPHASIC GROWTH MODEL AS AN EXAMPLE

The LM uses a theoretically and empirically derived energy allocation framework to describe the lifetime growth of fishes (Lester et al., 2004). The LM is founded on the common principle (Table 1) that maturation in fishes represents a change in energy allocation such that lifetime growth is in two phases: one before maturity and one after.

TABLE 1 A chronological summary of biphasic growth models that have been proposed for, or are commonly applied to, fishes

Reference	Type	Phase 1	Phase 2	Transition	Biological motivation, justification, or explanation
Brody (1945)	Discrete	Exponential	VB	At maturity	Investment in reproduction
Roff (1983)	Continuous	Linear	Curvilinear	Increase in the proportion mature with age	Investment in reproduction
Condrey, Beckman, and Wilson (1988)[a]	Discrete	VB	VB	k and t_0 change at some age	Growth changes with age
Bayliff, Ishizuka, and Deriso (1991)	Discrete	VB or Gompertz	Linear	At some length	Growth changes with age
Hoese, Beckman, Blanchet, Drullinger, and Nieland (1991)	Continuous	VB	VB	l_∞ increases with age	Growth changes with age
Soriano, Moreau, Hoenig, and Pauly (1992) models 1 and 2	Continuous	VB	VB	l_∞ or k increase with age	Diet shift
Soriano et al. (1992) model 3	Discrete	VB	VB	l_∞ and k change at some age	Diet shift
Rijnsdorp and Storbeck (1995); Baulier and Heino (2008)	Discrete	Linear	Linear	Slope and intercept change at maturity	Investment in reproduction
Craig, Choat, Axe, and Saucerman (1997)[a]	Discrete	VB	VB	l_∞, k and t_0 change at maturity	Investment in reproduction
Day and Taylor (1997)	Discrete	Power	VB	At maturity	Investment in reproduction
Charnov, Turner, and Winemiller (2001)	Discrete	Curvilinear[b]	Curvilinear[b]	Investment in reproduction terms added at maturity	Investment in reproduction
Laslett, Eveson, and Polacheck (2002)	Continuous	VB	VB	k increases with age	Habitat shift
Porch, Wilson, and Nieland (2002)	Continuous	VB	VB	k decreases with age	Ontogeny or habitat
Hearn and Polacheck (2003)	Discrete	VB	VB	l_∞ and k change at some age	Growth changes with age
Lester et al. (2004)	Discrete	Linear	VB	At maturity	Investment in reproduction
Tracey and Lyle (2005)	Discrete	VB	VB	l_∞, k and t_0 change at some age	Habitat shift
Quince et al. (2008a,b); Boukal et al. (2014)	Continuous	Curvilinear	Curvilinear	Investment in reproduction increases with age	Investment in reproduction
Alós et al. (2010)	Discrete	VB	VB	k changes at some age	Growth changes with age (perhaps due to investment in reproduction)
Mollet et al. (2010); Brunel et al. (2013)	Continuous	Curvilinear[b]	Curvilinear[b]	Investment in reproduction term increases with age	Investment in reproduction
Ohnishi, Yamakawa, Okamura, and Akamine (2012)	Discrete	VB	VB	Investment in reproduction term added at maturity	Investment in reproduction
Ohnishi et al. (2012)	Continuous	VB	VB	Investment in reproduction term increases with age	Investment in reproduction
Scott and Heikkonen (2012)	Continuous	Linear	Linear	Slope and intercept change with age	Investment in reproduction
Trip, Clements, Raubenheimer, and Choat (2014)	Discrete	VB	VB	Parameters change at some age	None given
Minte-Vera et al. (2016)	Continuous	VB	VB	Asymptotic size increases with age	Investment in reproduction
Minte-Vera et al. (2016)	Continuous	VB	VB	Investment in reproduction term added at maturity	Investment in reproduction

Discrete models describe two distinct growth phases, and continuous models describe a smooth transition between growth phases. VB refers to some version of the von Bertalanffy growth model, and l_∞, k and t_0 are the typical VB parameters.

[a]An identical model was developed by Fiorentino, Gancitano, Gancitano, Rizzo, and Ragonese (2013).

[b]Based on the metabolic theory of ecology (see West, Brown, & Enquist, 2001).

The key assumptions of the LM are that growth is indeterminate, body mass increases with length cubed, gonad mass is proportional to somatic mass, and metabolism scales with mass to the two-thirds power (Lester et al., 2004). Although this last assumption is debatable (Glazier, 2010; West, Brown, & Enquist, 1997, 1999) and can be relaxed (Boukal et al., 2014; Quince, Abrams, Shuter, & Lester, 2008a), it simplifies model derivation and fitting. The LM performs well for species that mature relatively late and have long reproductive life spans (Lester et al., 2004), and is effective at describing the lifetime growth of numerous fishes (Shuter et al., 2005) and perhaps other ectotherms (Honsey et al., 2017).

The LM describes immature growth in the lead-up to maturity as a straight line and mature growth as a von Bertalanffy curve:

$$l_t = h(t - t_1) \text{ when } t \leq T, \tag{1}$$

$$l_t = l_\infty \left(1 - e^{-k(t-t_0)}\right) \text{ when } t > T, \tag{2}$$

where l_t is length at time t, h is juvenile growth rate (length per unit time), t_1 is the LM (immature) hypothetical age at length 0, T is last immature age (LM parameter for age-at-maturity), l_∞ is asymptotic length, k is the von Bertalanffy (Brody) growth coefficient, and t_0 is the von Bertalanffy (adult) hypothetical age at length 0. Lester et al. (2004) further showed that l_∞, k and t_0 reflect known trade-offs between growth, reproduction and mortality:

$$l_\infty = \frac{3h}{g}, \tag{3}$$

$$k = \ln\left(1 + \frac{g}{3}\right), \tag{4}$$

$$t_0 = T + \frac{\ln\left(1 - \frac{g(T-t_1)}{3}\right)}{\ln\left(1 + \frac{g}{3}\right)}, \tag{5}$$

where g is the cost to somatic growth of maturity (often assumed to be dominated by investment in reproduction; Kozlowski, 1996; Roff, 1983), and that

$$g \approx 1.18(1 - e^{-M}), \tag{6}$$

$$T \approx \frac{1.95}{e^M - 1} + t_1, \tag{7}$$

where M is the instantaneous rate of late-stage juvenile and adult natural mortality. The parameter g captures the proportion of surplus energy allocated into direct (e.g. gonadal development) and indirect (e.g. migration, nesting, displaying, metabolic costs of storing gonads) reproductive investment—for further discussion, see Boukal et al. (2014, section 2.3).

We use the LM to demonstrate biphasic fitting techniques because it is grounded in theory, empirically supported, popular, and exhibits many of the challenges that are encountered when fitting a biphasic model. Unlike uniphasic models, biphasic models are usually selected and applied based on a priori information about how and when growth transitions between phases (Table 1). If this information is available, then it must then be incorporated properly

into the model. For example, the LM uses the last immature age (T) to differentiate between growth phases, but empirical data usually describe age-at-first-reproduction (i.e. some age > T). Model parameter estimates can also depend on whether a transition point, such as maturity, is estimated in advance or as part of the model-fitting procedure (Minte-Vera et al., 2016). Such dependencies often stem from confounded and correlated parameters, especially when estimates are uncertain and sensitive to starting values. Other examples include the Mollet et al. (2010) model and modified versions of the LM (Boukal et al., 2014; Quince et al., 2008a,b), all of which can generate variable or biased parameter estimates, or simply fail to converge. Although the correlated parameters in the LM and related biphasic models are statistically inconvenient, they result from important life-history trade-offs and general ecological rules. Many biphasic models incorporate these trade-offs and correlations into the model structure based on empirical relationships between natural mortality and life-history parameters (e.g. Equations 6 and 7 above). Hence, biphasic models can be more realistic than uniphasic models that assume that traits are independent and fixed, and they represent an opportunity to improve ecological and management inference through insight into life-history traits, vital rates and empirical proxies (e.g. the gonadosomatic index as a proxy for reproductive investment).

3 | TECHNIQUES

The first factor to consider when fitting a biphasic model is whether the data meet model assumptions. For example, immature growth can be nonlinear (particularly in early life) due to ontogenetic diet shifts, changes in per capita food availability and other factors (Lester et al., 2004), which would violate the assumptions of the LM. One may therefore need to modify the model (Quince et al., 2008a) or truncate the data accordingly (McDermid, Shuter, & Lester, 2010). One must also consider the structure of the data: Are they cross-sectional (snapshot of a population at one time point) or longitudinal (repeated measures through time)? If the latter, do the data track individuals or cohorts? Do they describe single or multiple populations? The framework used to fit a biphasic model also depends on whether data are available to describe the shift in growth (e.g. maturity data for the LM) and on whether one wishes to include environmental predictors or other variables that might help to explain growth.

In this section, we address many of the considerations mentioned above by introducing and evaluating some techniques for fitting biphasic models across a variety of scenarios. We focus on maturity-based biphasic models and use the LM as an example. We first describe potential discrepancies in the meaning of "maturity" between models and data. We then highlight different approaches for fitting biphasic models. We organize this section according to model complexity, beginning with the simplest fits (fitting the LM with maturity data) and moving to more complex approaches (hierarchical modelling across populations without maturity data). We provide companion code in appendices throughout.

3.1 | Fitting biphasic models with maturity data

When incorporating maturity data in a biphasic fit, one must account for potential differences in the meaning of "maturity" between the model and the data. For instance, the LM assumes that growth slows in response to energetic investment in reproduction rather than a reproductive event (e.g. spawning or breeding). The onset of investment in reproduction often occurs before maturity is assessed. In longer-lived bony fishes, for example, investment in reproduction can occur a year or more before first spawning, and maturity in chondrichthyans usually corresponds to the mean age at which individuals are physically capable of reproducing (Cotton, Dean Grubbs, Dyb, Fossen, & Musick, 2015). Lags between the onset of investment in reproduction and maturity data or metrics (e.g. age-at-50%-maturity or A_{50}) should be corrected for before fitting maturity-based biphasic models. For example, if initial investment in reproduction occurs in the year prior to when age-at-maturity is assessed, and if individual ages are in integer years, then $T = A_{50} - 1$.

Energetic constraints and life-history trade-offs often truncate parameter distributions that are dependent on another estimated parameter. This stochastic truncation can be difficult to account for with typical model-fitting approaches. For example, assuming that g in the LM is constant with age, an individual cannot allocate more surplus energy into reproduction than was available for somatic growth in the juvenile phase. Analytically, g has an intrinsic maximum and is bounded between 0 and $3/(T - t_1)$. Such constraints can lead to errors in optimization routines, particularly if parameter distributions are not appropriately bounded during estimation (e.g. penalized likelihoods or truncated distributions), and may cause other errors (e.g. nonpositive definite Hessian matrix). In a maximum likelihood framework, one can estimate on log(g) or logit(g) to constrain estimation and set a penalty to the likelihood if g exceeds $3/(T - t_1)$.

The most intuitive approach to fitting the LM with maturity data is to fit the two growth phases in sequence (Appendix S1). For example, one can subset the data into immature and mature individuals, fit a linear model to the immature subset (Equation 1) and then treat the parameter estimates from the immature fit as fixed when fitting the mature curve (Equation 2). Fitting the model in this manner requires an a priori estimate of age-at-maturity (e.g. A_{50}) to substitute for T. This simplistic approach may be necessary if data are limited for one or both phase(s) of growth. However, this approach restricts error propagation, which can complicate parameter estimation and lead to erroneous conclusions.

Estimates of age-at-maturity can also be incorporated into full model fits as a known breakpoint (e.g. substituting A_{50} for T). Parameter estimation can be carried out in either a maximum likelihood (Appendix S2) or Bayesian framework. This approach allows for better error propagation than the previous method but is still limited given that age-at-maturity is fixed. In addition, this method can be sensitive to starting values and may require some form of restriction on parameter estimates (e.g. penalized likelihoods) to maintain realistic parameter combinations.

The most inclusive method for fitting a biphasic model with maturity data is to estimate maturity using a maturity ogive that complements the growth model. This maturity model can be optimized on a joint likelihood (or posterior) alongside the biphasic model (see Matthias, Ahrens, Allen, Lombardi-Carlson, & Fitzhugh, 2016; Quince et al., 2008b; Ward, Post, Lester, Askey, & Godin, 2017). This method allows for improved estimates of variance around parameters because the errors and correlations among parameters are allowed to trade-off naturally among model subcomponents. The downside of this approach is that it typically requires customized coding, more computational time and assumptions regarding the shape and symmetry of the maturity ogive. Because estimation using this approach relies on the quality of maturity data, errors in the maturity data (e.g. mature but nonreproducing adults may be difficult to distinguish from juveniles) can lead to biased parameter estimates.

3.2 | Fitting biphasic models without maturity data

If maturity data are unavailable, then age-at-maturity can be estimated directly from size-at-age data using maturity-based biphasic models (Table 1). The shift in growth at maturity should lead to detectable changes in model residuals, thus allowing for estimation of age-at-maturity. For example, the sizes-at-age of mature fish are less likely to adhere to predictions from the immature growth phase than the adult phase and vice versa. However, estimating age-at-maturity can be problematic for many biphasic models because it is highly correlated with other parameters and can be confounding (Brunel, Ernande, Mollet, & Rijnsdorp, 2013; Minte-Vera et al., 2016; Mollet et al., 2010).

We simulation-tested the relative performance of three approaches for fitting the LM without maturity data: penalized maximum likelihood (Appendix S3), likelihood profiling (Honsey et al., 2017; Appendix S4) and Bayesian Markov chain Monte Carlo (MCMC; Appendix S5). The simulation tested all combinations of three levels each for adult natural mortality rate (M = {0.1, 0.2, 0.5}, per year) and the coefficient of variation in length-at-age (cv_l = {0.1, 0.15, 0.25}). Other parameters were held constant across simulation scenarios (t_1 = −0.2 year, h = 50 mm/year, slope of age-dependent selectivity = −0.4). The g and T parameters were calculated as functions of M (using Equations 6 and 7, respectively), and the age-at-50%-selectivity was equal to T. We then used a multinomial observation process to generate realistic samples (n = 50) of population age and size structures. The resulting length-at-age data are similar to what might be observed in wild populations. We evaluated the performance of the three methods to estimate the true growth parameters using a bootstrap approach (N_{boot} = 100) and calculated the root-mean-square error (RMSE) per bootstrapped iteration:

$$\text{RMSE} = \sqrt{\frac{1}{n} \Sigma_{i=1}^{n} (\hat{l}_i - l_i)^2}, \tag{8}$$

where n is the total number of fish, l_i is the observed length of fish i, and $\hat{l}_i$ is the maximum likelihood (or posterior mean) predicted length

for fish *i*. Lower RMSE values indicate low bias and high precision. We evaluated the ability of each method to recover true life-history parameters θ using per cent bias:

$$\text{Bias}_\theta = \frac{\theta - \hat{\theta}}{\theta} 100\%, \tag{9}$$

where $\hat{\theta}$ is the maximum likelihood (or posterior mean) estimate of the parameter. Although this approach does not capture bias for each parameter's 95% quantile, it does indicate the general performance of each method to estimate specific parameters. Lastly, we tested the sensitivity of each method to a range of starting values. Figure 2 shows results for a single iteration of the simulation, including the true life-history parameters, inducing observation error and evaluating model performance (Appendix S6).

The likelihood profiling and Bayesian MCMC approaches were relatively unbiased and precise (Figure 3; Appendix S7). In contrast, the penalized likelihood approach was sometimes biased and sensitive to starting values. Most of the uncertainty and bias in parameter estimates is in t_1, an intercept parameter with limited scope for ecological and evolutionary inference (but see Lester et al., 2004; Quince et al., 2008a). The relatively high bias in t_1 estimates likely stems from the nonlinear correlations among t_1 and the other parameters (e.g. relatively low bias in *h* can lead to high bias in t_1). All three methods performed worse when mortality rates were low (e.g. *M* = 0.10 per year) than when they were high, with the penalized likelihood approach being the least reliable under low natural mortality rates. This result likely stems from the fact that low adult natural mortality is correlated with low reproductive investment (Equation 6), leading to a subtle (and difficult to detect) change-point between juvenile and adult phases. Bias and precision in estimating specific life-history parameters were relatively equal for the likelihood profiling and Bayesian MCMC approaches (Appendix S7). Estimates of *T* and *h* were the most inconsistent across scenarios, particularly for the penalized likelihood approach. Per cent bias in *T* increased with increasing variance in length-at-age (and, in some cases, increasing mortality), while bias in *h* decreased with increasing mortality.

3.3 | Fitting biphasic models to data describing multiple populations

One may wish to estimate the growth of multiple populations simultaneously for several reasons, including to (1) propagate uncertainty and error trade-offs during estimation, (2) estimate environmental effects on growth trajectories (Helser & Lai, 2004; Shuter, Jones, Korver, & Lester, 1998), (3) gain insight into growth-associated traits and their trade-offs across environments and (4) estimate growth for data-limited populations alongside data-rich populations. Simultaneously estimating biphasic growth model parameters for multiple populations can be challenging. For instance, one must decide whether to assume that growth is related among populations (in which case the parameters should be hierarchical arising as random variables from a common distribution, i.e. a mixed-effects model), or that growth parameters among populations are independent (i.e. fixed effects model). When using a hierarchical approach, one must be aware of the "shrinkage

effect" (whereby the population-level parameter estimates are pulled towards the group mean), which can be especially large if samples are unbalanced across populations (Helser & Lai, 2004). Fixed effects approaches should be relatively straightforward adaptations of the hierarchical approaches and code that we discuss below.

Recent methods to estimate hierarchical models have become streamlined (Bolker et al., 2009, 2013), but many biphasic growth models have properties that make standard mixed-effects fitting approaches difficult to adopt (e.g. nonindependent phases, nonlinearity, correlated parameters, stochastic parameter bounds). Hence, the analysis must be coded manually. A relatively robust way to describe growth with a biphasic model is to numerically approximate growth parameter distributions using MCMC algorithms and Bayesian inference. Appendix S8 provides code for fitting the LM using a hierarchical Bayesian approach in the JAGS language (Plummer, 2003) via the RUNJAGS package in R (Denwood, 2016).

The simulation in Appendix S8 has input parameters for the number of populations, the maximum number of age classes and the mean and variance of growth parameters across populations. The latter two features are used to define a global (i.e. cross-population) distribution for a given life-history trait, from which population-specific values arise as random variables. We provide an example in which we simulate growth across 10 populations with an unbalanced design (sample sizes vary between 40 and 200 samples per population), assuming that each of the LM parameters is related among populations (Figure 4). Where appropriate, the parameter values were identical to the single population simulations above, and vague priors were used to fit the model. Our results indicate that the Bayesian hierarchical approach can recover the simulated parameter values despite strong correlations in the posterior parameter space (Figure 4f).

Adapting the LM for different scenarios requires relatively simple tweaks to the approaches described above. For example, a hierarchical framework (Appendix S8) can be used to fit biphasic models to longitudinal data (e.g. repeated measures of growth across individuals, with individual-level parameters treated as random deviances from a population-level mean). In addition, one can estimate the effect of environmental determinants on growth parameters using a Bayesian hierarchical analysis combined with a parameter inclusion probability (modelled as a latent variable; Royle & Dorazio, 2008). In Appendix S9, we demonstrate a simulation in which we use a hierarchical regression and inclusion probability approach to recover both population-specific growth rates and the slope in average growth rate across populations along an environmental gradient. The simulation mirrors those in Appendices S6–S8 to generate realistic, noisy data with an unbalanced sampling design. Using this approach, we recovered both true growth rates and the slope in average growth rate across populations (Figure 5). Modelling frameworks such as these can allow for broader ecological inference regarding trait–environment relationships.

4 | RECOMMENDATIONS

In this section, we make recommendations and highlight potential solutions for barriers that might arise when fitting biphasic models.
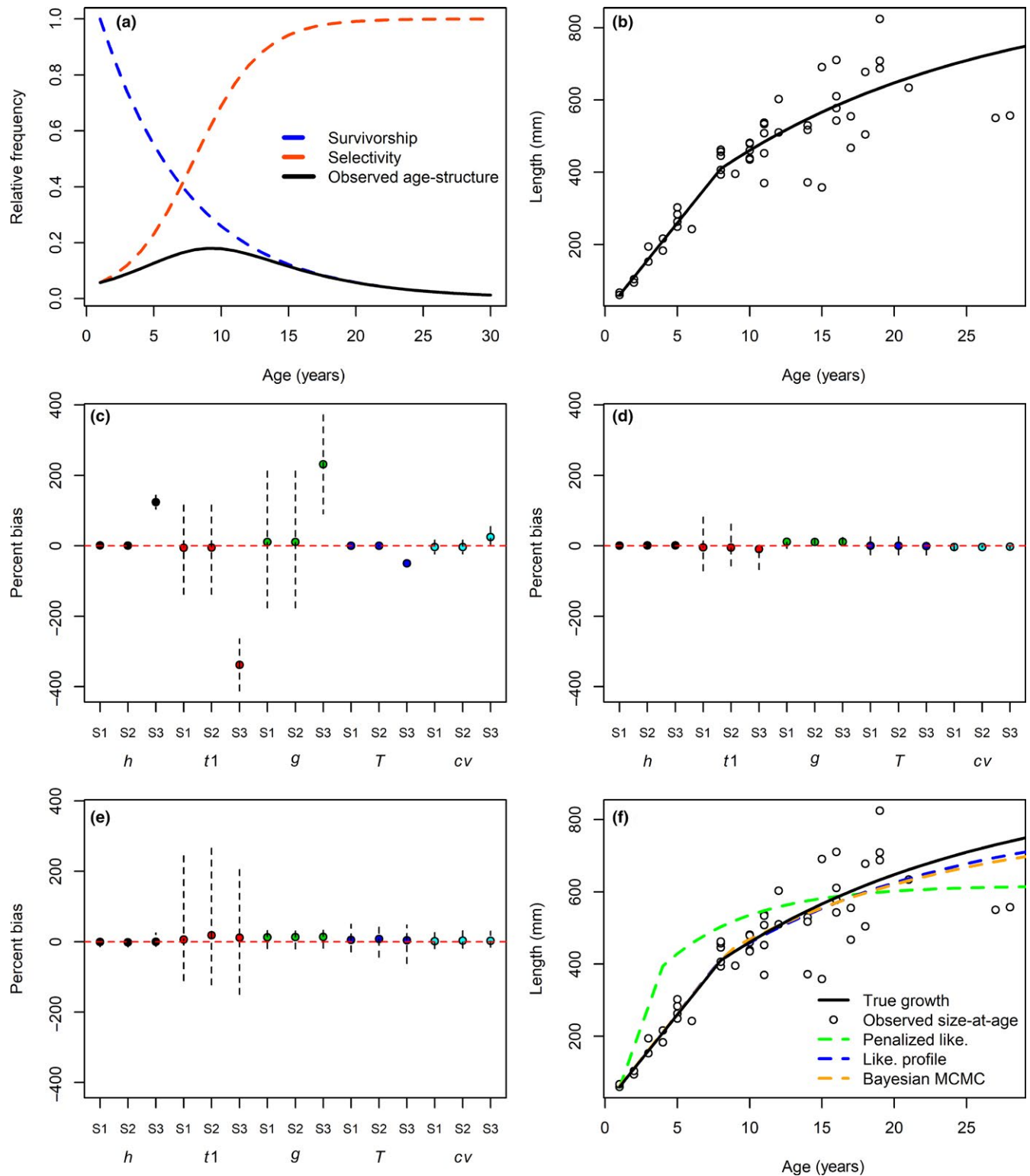
FIGURE 2 Results from a single iteration of the simulation test of three different statistical approaches for fitting the Lester biphasic growth model without maturity data (see Appendix S6). Data were simulated according to the Lester model with stochastic noise. (a) Sample sizes-at-age were based on survivorship (M = 0.15 per year) and gear selectivity to approximate realistic size and age structures. (b) Simulated data (n = 50) and "true" growth trajectory. (c–e) Mean per cent bias (points) and 95% confidence/credible intervals (dashed lines) for four Lester biphasic model parameters and the coefficient of variation in length-at-age (cv) fit using (c) penalized maximum likelihood, (d) likelihood profiling and (e) Bayesian MCMC. Three different vectors of starting values (S1 = below true h, S2 = close to true h, S3 = above true h) were used to evaluate the sensitivity of each approach to starting values. (f) Mean estimated growth trajectory from each approach fitted under S3 starting values compared to the true growth trajectory
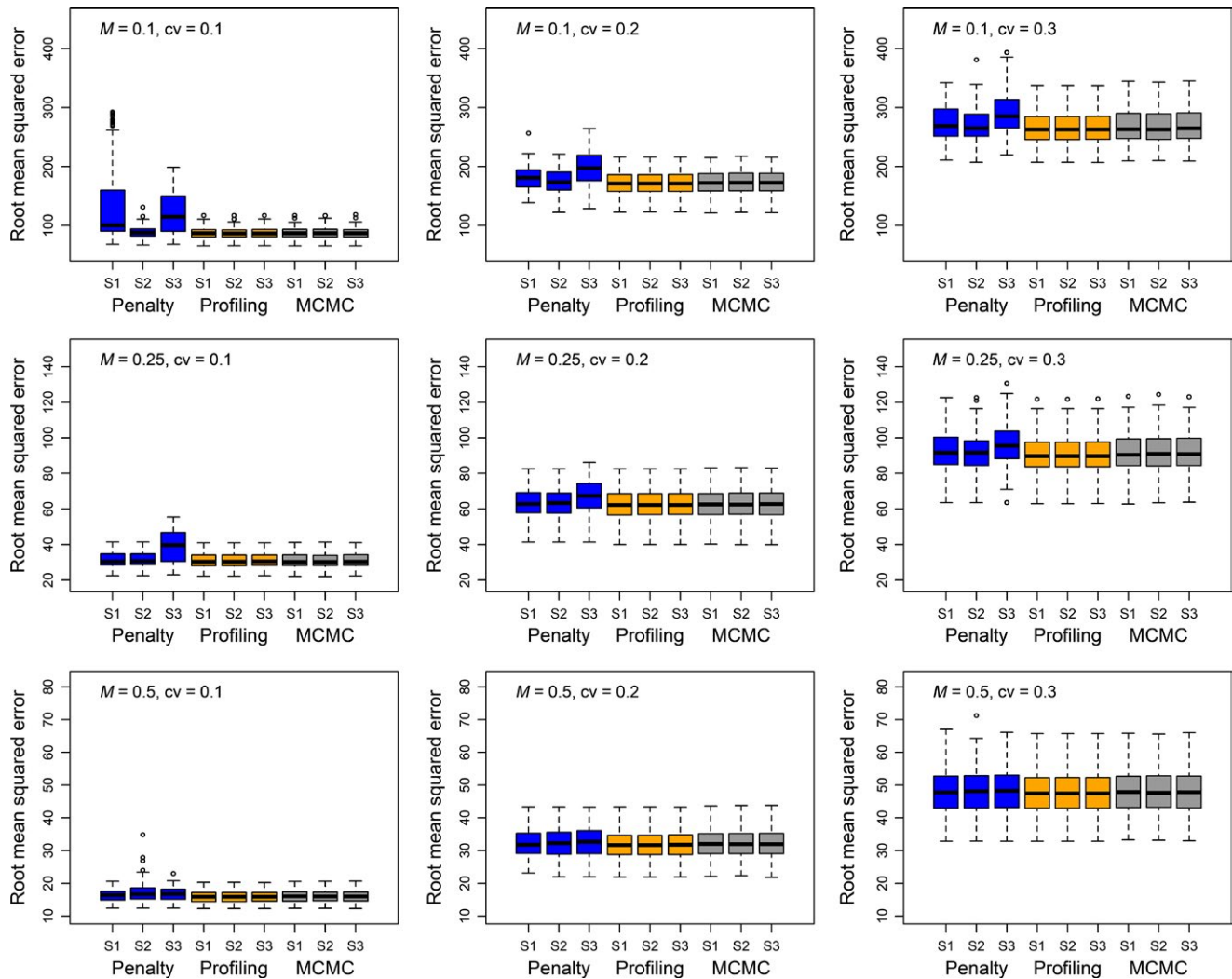
FIGURE 3 Relative performance of three approaches for fitting the Lester biphasic model without maturity data (blue = penalized maximum likelihood, orange = likelihood profiling, grey = Bayesian MCMC) evaluated by root-mean-squared error for 100 bootstrapped datasets across nine scenarios (natural mortality M = {0.1, 0.2, 0.5} per year and coefficient of variation in length-at-age cv_l = {0.1,0.15,0.25}). Other parameters were held constant across scenarios. Box and whiskers show median (black bars) and 95% quantiles. Each approach was initialized using three different vectors of starting values (S1 = below true h, S2 = close to true h, S3 = above true h) to evaluate the sensitivity of each approach to starting values (see Appendix S7 for details and additional results)

Our most general recommendation is to start with simpler approaches (relative to the coding expertise of the practitioner and quality of the data) before adding complexity. This includes starting by penalizing parameter estimates on reasonable bounds (and perhaps iteratively relaxing or tightening these bounds) because the sensitivity and correlations between parameters can lead to errors during estimation (Minte-Vera et al., 2016; Mollet et al., 2010). If parameter correlation continues to be problematic, or accounting for that correlation is of interest, then we recommend drawing parameter estimates from a multivariate normal distribution and estimating a covariance matrix between parameters (Helser & Lai, 2004). This approach can speed up estimation, and most MCMC algorithms can incorporate multivariate distributions. We also recommend varying starting values and re-fitting the model to assess whether parameters converge on a common estimate.

When maturity data are available, we recommend jointly estimating a maturity ogive and biphasic growth model. This approach is generally more robust and statistically appropriate than estimating age-at-maturity a priori, and it allows for better error propagation when estimating parameters. Simulation tests of this technique can be found in Quince et al. (2008a), and example applications can be found in Quince et al. (2008b) and Matthias et al. (2016).

We encountered differences in ease of use, accuracy, precision, speed and robustness among the three approaches that we tested for fitting the LM without maturity data. We recommend choosing a method based almost entirely on accuracy, performance and robustness, even though some methods trade-off one attribute against another (e.g. robustness vs. speed). The penalized likelihood approach is a quick and relatively easy way to fit biphasic models without maturity data. However, we recommend against using this approach for formal
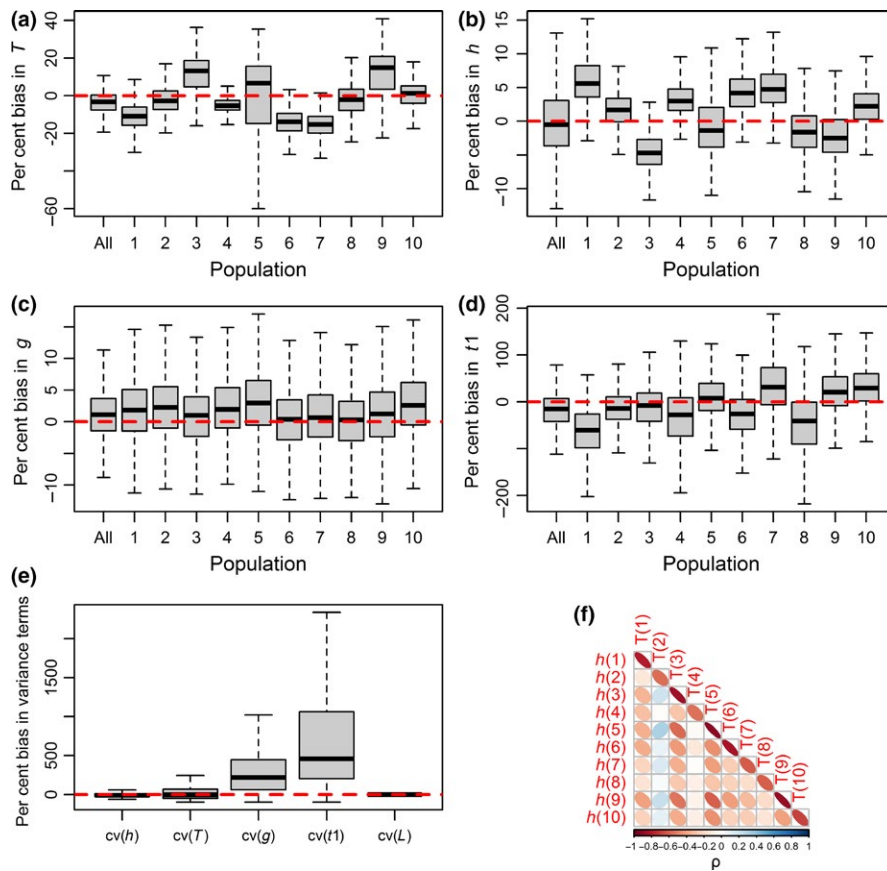
FIGURE 4 Multipopulation Lester model estimation using the Bayesian hierarchical MCMC approach in JAGS. Black bars represent posterior medians, and dashed lines represent 95% credible intervals. The red line indicates the true simulation parameters (zero bias). Ten populations were simulated with varying Lester model parameters and unbalanced sample sizes (n = 40–200 individuals per population). (a–d) Per cent bias in Lester model parameter estimates. (e) Per cent bias in variance terms for Lester model parameters and size (L) across all populations. (f) Correlations between two parameters, T (age-at-maturity) and h (juvenile growth rate), for each of the 10 populations
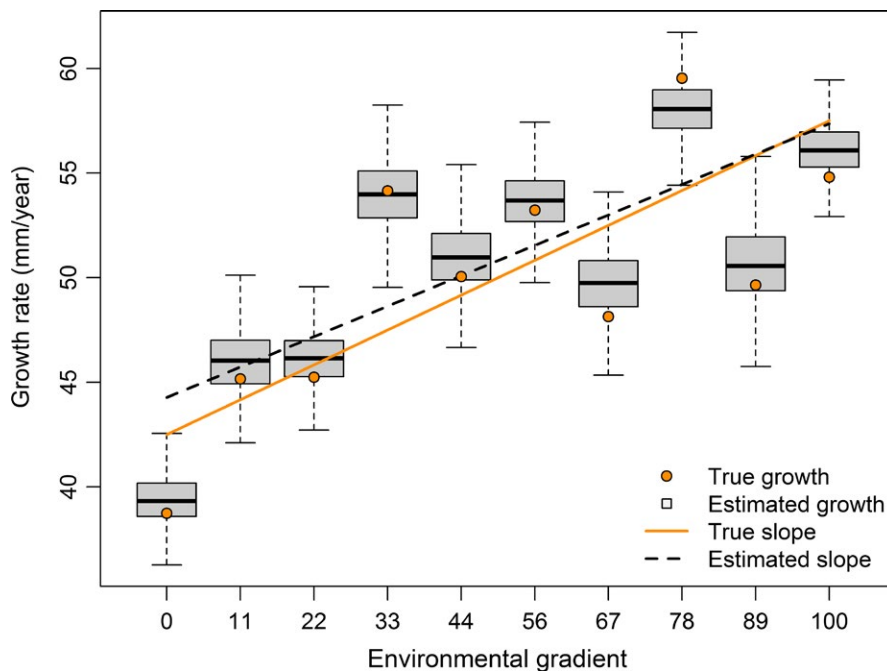

FIGURE 5 Multipopulation growth simulation in which average growth rate increases along some environmental gradient. Lester models were fit using a Bayesian hierarchical method with a parameter inclusion probability approach (Appendix S9). Box and whiskers show the median and 95% credible intervals for the posterior distribution for growth rate for each population; points denote the simulated true growth rates. The estimated environmental trend on average growth rate (posterior mean slope, dashed black line) reflects the true trend (solid orange line)

assessments and ecological inference unless data quality is high (e.g. large sample sizes). We instead recommend either the likelihood profiling or Bayesian MCMC approaches because they more consistently provide accurate parameter estimates. Likelihood profiling was slower and required more manual coding than penalized maximum likelihood, but was faster and arguably easier to code than the Bayesian MCMC method. The MCMC approach readily accommodates more complex applications (e.g. hierarchical models) but is slower and can be more difficult to implement and validate given the added challenge of choosing prior distributions (e.g. informative vs. diffuse, normal vs. uniform, etc.). Aside from philosophical differences between Bayesian and frequentist inference, any further differences are primarily in

implementation and coding. The ease of use for any particular method will depend on one's experience (e.g. familiarity coding in MCMC software). We encourage the use of the R code provided in the appendices as a starting point for implementing all of the approaches discussed herein.

We recommend hierarchical approaches for more complex applications of biphasic growth models, including fits to repeated-measures (e.g. back-calculated) data and estimating environmental trends across multiple populations. Nonlinear mixed-effect models can be coded in both Bayesian and frequentist frameworks in a variety of statistical languages. Bayesian approaches are useful because (1) they can incorporate prior information, (2) MCMC algorithms are typically stable and allow for errors in model components to trade-off naturally, and (3) latent variable and mixture-model approaches can be incorporated in most Bayesian MCMC software (Royle & Dorazio, 2008), which increases the flexibility (and potential complexity) of biphasic model applications and allows one to address interesting eco-evolutionary questions (see Matthias et al., 2016). When using Bayesian MCMC approaches, we strongly recommend assessing whether the model has converged on a stable posterior mode (Gelman et al., 2013) using tools such as posterior convergent diagnostics, residual diagnostics and goodness-of-fit tests (e.g. posterior predictive checks, Bayesian P-values).

5 | CONCLUSIONS

The convention in fish science and other disciplines is to fit a single growth curve to size-at-age data across years and cohorts. However, advances in life-history theory, statistical methods and computational power have paved the way for fitting more complex growth models (Lorenzen, 2016), thus improving both our basic understanding of growth across taxa and the efficacy of management. These advances are evident in the many flexible and cutting-edge adaptations of growth models (Maunder, Crone, Punt, Valero, & Semmens, 2016).

We presented techniques, recommendations and code for fitting biphasic growth models across a range of scenarios. These models can accurately describe growth while providing important and direct inference on life-history traits. These advantages result from common life-history principles and trade-offs and should therefore extend to many species that exhibit indeterminate growth (Honsey et al., 2017). We chose the LM as our example model because it is rooted in life-history theory and popular in the literature, particularly for trait-based and eco-evolutionary inference (Alós, Palmer, Balle, Grau, & Morales-Nin, 2010; Nakayama et al., 2017; Uusi-Heikkilä et al. 2016; Ward et al., 2017). However, our recommendations apply to many other biphasic models (e.g. diet and habitat shifts can be modelled much like maturity; Table 1). These models have the potential to improve our understanding of growth and life history across taxa and can be adapted to a variety of interesting applications. Importantly, evaluations of these models (Minte-Vera et al., 2016 and this manuscript) show that certain model-fitting

approaches can lead to biased parameter estimates, suggesting that different models and approaches can have consequences for parameter inference. We encourage both the increased application of biphasic models and robust assessments of their ability to describe growth and life history across taxa, conditions and scenarios.

AUTHORS' CONTRIBUTIONS

K.L.W. and P.V. conceived of the idea for the manuscript; K.L.W. organized and led the project; K.L.W., A.E.H., B.M. and P.V. wrote the manuscript; K.L.W., A. E. H. and B.M. provided code and Markdown documents; K.L.W., A.E.H. and P.V. designed figures and tables.

DATA ACCESSIBILITY

All simulated data used in this manuscript are available via our R code supplemental files (https://doi.org/10.5281/zenodo.1044474); no empirical data were used in this manuscript.

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