



# Comparison of growth models for sequential hermaphrodites by considering multi-phasic growth



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## ARTICLE INFO

### Article history:

Received 26 October 2015

Received in revised form 3 February 2016

Accepted 4 February 2016

Available online 20 February 2016

### Keywords:

Sex change

von Bertalanffy growth

Multi-phasic growth

Management reference points

Gag grouper

## ABSTRACT

The von Bertalanffy (VB) growth model has been extensively used to describe fish growth. However, it may not be the best predictor of lifetime growth patterns for fish with complex life history (e.g., hermaphroditism). We sought to determine if growth models accounting for maturity and sex change were more appropriate than the VB model at capturing the growth and maturation patterns of Gag *Myceteroperca microlepis*, a protogynous hermaphrodite. To account for changes in growth at maturity, we used the Lester et al. (2004) growth model (bi-phasic Lester) and a modified Lester et al. (2004) model to account for an additional growth phase at sex change (tri-phasic Lester). We also compared management reference points from each model using a yield-per-recruit (YPR) framework. The tri-phasic Lester model described growth and reproductive schedules better than the bi-phasic Lester or VB models, indicating separate growth phases associated with maturation and sex change. Estimates of  $F_{MAX}$  from the YPR analysis were lower when using the tri-phasic Lester model ( $0.21 \text{ year}^{-1}$ ) compared to the VB model ( $0.33 \text{ year}^{-1}$ ) when growth parameters were linked to natural mortality. Fishing mortality rates resulting in 35% of unfished total and male-specific spawning stock biomasses-per-recruit were similar for all models, but female-specific estimates were lower using the bi-phasic Lester model. Reference points from the VB model were generally lower compared to either Lester model using natural mortality rates that were not tied with the growth parameters. Our results support arguments that a single growth curve is insufficient to capture lifetime growth of fish. However, growth curves from the VB and tri-phasic Lester models were similar for all ages, especially less than age 12. This suggests the VB model can be used to describe mean length-at-age when information on reproductive status is not available, but may result in inappropriate management recommendations.

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## 1. Introduction

The von Bertalanffy growth model (hereafter referred to as VB; von Bertalanffy, 1938) has been extensively used to describe growth of fish and other taxa that display indeterminate growth (Ricker, 1975; Lester et al., 2004). One of the main advantages of the VB model is its strong biological and empirical support (Beverton and Holt, 1957; Chen et al., 1992; Lester et al., 2004). However, this model has been criticized because it seems unlikely that one growth curve should be able to represent the complex physiological changes happening throughout the life of an organism (Day and Taylor, 1997; Czarnołe'ski and Kozłowski, 1998; Lester et al., 2004). The VB model is relatively inflexible as it considers only decreas-

ing incremental growth throughout the life of the organism, which may not hold true for very young fish (e.g., larval and early juvenile growth phases; Beverton and Holt, 1957; Ricker, 1975; Walters and Martell, 2004). More recently the model has been criticized because it does not account for changes in energy allocation to reproduction after a fish reaches maturity (Charnov, 1993; Charnov et al., 2001; Lester et al., 2004). This suggests that using the VB model can lead to misspecification of management reference points and could result in over- or under-exploitation because the VB model ignores potential changes in growth patterns before and after maturation.

Accurately estimating life history parameters, such as growth and reproductive schedules, are crucial to management because these traits are often used to develop size-based regulations (e.g., size limits, harvest slots, etc.), to set harvest limits, and are major components in fisheries assessment models (Ricker, 1975; Jennings et al., 2001; Radomski et al., 2001; Walters and Martell, 2004). Commonly, fish growth is estimated independently of reproduc-

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tive schedules (e.g., length or age at maturation), where growth is assumed to follow the VB model and estimates of age/length at maturation are obtained using a logistic regression. This process assumes that age and length interact to influence the timing of maturation via: (1) the relationship between age and length or (2) directly accounting for the growth variation by estimating both age and length regression coefficients. This ignores any interaction between maturity and growth, even though it has been shown that both the timing of maturation and the amount of energy allocated towards reproduction may influence lifetime growth (Charnov, 1993; Charnov et al., 2001; Lester et al., 2004). There are numerous examples of growth models that incorporate the influence of maturity on growth (e.g., Brody, 1945; Lester et al., 2004) and assume that fish grow according to multiple phases throughout their life. One such example, developed by Lester et al. (2004), assumes a period(s) of linear growth prior to maturation (i.e. no reproductive investment) and growth following the VB model after maturation. Because this and similar models incorporate the age at maturation as a parameter, changes in the timing of or biased estimates of maturity can have large impacts on the subsequent growth curves.

Thus, fish experiencing physiological or behavioral changes after maturity, such as sexual transition, should experience an additional growth phase once individuals change sex. This is because the energetic costs of producing eggs are markedly higher than those of producing sperm (Asher et al., 2008). Therefore in protogynous hermaphrodites (individuals initially mature as female), females that have transitioned to male will have additional energy resources to devote to either growth or to mate acquisition (St. Mary, 1994; Chu and Lee, 2012; Cogalniceanu et al., 2013). Additionally males often suffer from high energetic costs and increased mortality due to increased levels of aggression and resource defense, reduced time foraging, or fasting during mating season (e.g., Neuhaus and Pelletier, 2001; Hoffman et al., 2008; Georgiev et al., 2014). However these changes associated with sex change are often ignored when estimating growth because many authors use the VB model to describe growth rates (for examples see: Buxton, 1992; Garratt et al., 1993; Alonzo and Mangel, 2004; Alonzo et al., 2008; Cossington et al., 2010; Linde et al., 2011; Fenberg and Roy, 2012).

It is important to consider models other than the VB to describe the complex changes happening throughout the life of a sex-changing fish as a result of the physiological and behavioral changes likely associated with sex change. Several authors have modified the VB model to explain the sexual-size dimorphism observed in many sex-changing species (Garratt et al., 1993; Adams and Williams, 2001; Munday et al., 2004; Linde et al., 2011), but have largely ignored the physiological and behavioral changes also associated with changing sex. Garratt et al. (1993) developed a bi-phasic VB model that described accelerated growth after transition (i.e. a growth spurt). However this model did not incorporate changes associated with maturation. Several authors back-calculated length-at-age estimates to compare the growth rates of fish that had changed sex to those that were still the primary sex, but did not assess potential changes in growth due to maturation or sex change (e.g., Adams and Williams, 2001; Munday et al., 2004; Linde et al., 2011). We sought to expand on these studies by modifying the Lester et al. (2004) growth model to account for an additional growth phase associated with sex change. Our primary objective was to determine if accounting for just maturity (i.e. the bi-phasic model developed by Lester et al. (2004)) or accounting for growth transitions associated with maturity and sex change (i.e. tri-phasic Lester) would more accurately describe the growth patterns of a protogynous hermaphroditic fish than the standard VB model. Our second objective was to compare management refer-

ence points from each model using a yield-per-recruit framework to determine the implications of using each growth model.

## 2. Methods

We used the Gulf of Mexico Gag *Mycteroperca microlepis* as a case study for this analysis. Gag is a long-lived (maximum observed age 31 years) protogynous hermaphrodite. Gag are targeted in both commercial and recreational fisheries. Gag length (fork length in mm), age, and histology data were obtained from fisheries-dependent and -independent samples between 1979–2012 from the National Marine Fisheries Service (NMFS) used in the 2013 Gag stock assessment (SEDAR, 2014). Gag length-, maturity-, and sex change-at-age data were fit using a Bayesian hierarchical framework to predict growth using VB, bi- and tri-phasic Lester models, and timing of maturation and sex change assuming logistic functions. Growth models were run in program R version 3.1.3 using runjags version 3.3.0 (Denwood, 2013; R Development Core Team, 2013) and yield-per-recruit models were run in program R version 3.1.3 (R Development Core Team, 2013). All equations for the growth models and yield-per-recruit equations are presented in Tables 1 and 2 respectively.

The data came from multiple fishery-dependent sources (~31,700) and fishery-independent surveys (~1500). Because of the selectivity of the fishery-dependent sources, growth was modeled in the recent Gag assessment using a truncated normal distribution with a constant standard deviation to account for minimum length limits in commercial and recreational fisheries (developed by McGarvey and Fowler, 2002; SEDAR, 2014). Additionally, they used a modified VB model that assumed a period of linear growth from age-0 (fixed at 100 mm) to age-1 (SEDAR, 2014). We chose to use the traditional formulation of the VB model incorporating an age-specific standard deviation in order to reduce model complexity and avoid the assumption of a constant standard deviation. Because there were samples of small, young fish from fishery independent surveys (~1750 less than 500 mm and almost 300 less than age-1), data were aggregated without any consideration for sample sizes within each gear type following the recommendations of Wilson et al. (2015). As shown in Wilson et al. (2015), when there are samples of small, young fish, this method helps account for some of the effects of gear selectivity on growth parameter estimation.

### 2.1. Growth models

Mean length-at-age from the VB model was estimated using the standard formulation of the von Bertalanffy growth equation; where  $L_{\infty}$  is the average maximum attainable length,  $k$  is the Brody growth coefficient scaling size to catabolism, and  $t_0$  is the theoretical length-at-age 0 if the fish always grew according to the VB model (Eq. (1); Table 1). For the bi-phasic Lester model, mean length-at-age was estimated using the growth model developed by Lester et al. (2004); where  $h$  is the pre-reproductive growth rate,  $t_1$  is the age intercept for the pre-reproductive growth phase, and  $T$  is age at maturity (Eq. (2); Table 1). The Lester et al. (2004) formulation also estimates reproductive investment ( $g$ ), which is used to estimate  $k$  and  $L_{\infty}$  in the post-maturation growth phase (Eq. (2); Table 1). The tri-phasic Lester model is identical to the bi-phasic Lester, except there is an additional growth phase after transition to male at age  $\tau$  and sex-specific estimates of  $g_s$ ,  $k_s$ , and  $L_{\infty,s}$  (Eq. (3); Table 1). We assumed length-at-age was normally distributed with a constant coefficient of variation (Eq. (4); Table 1).

Age-based maturity  $m_{a,i}$  and sex change  $D_{a,i}$  for individual  $i$  was described using Bernoulli trials with age-specific probabilities of being mature or male (Eqs. (7) and (8); Table 1). Age-specific prob-

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