Generalised growth models for aquatic species with an application to blacklip abalone (*Haliotis rubra*)

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ABSTRACT

This paper presents a maximum likelihood method for estimating growth parameters for an aquatic species that incorporates growth covariates, and takes into consideration multiple tag-recapture data. Individual variability in asymptotic length, age-at-tagging, and measurement error are also considered in the model structure. Using distribution theory, the log-likelihood function is derived under a generalised framework for the von Bertalanffy and Gompertz growth models. Due to the generality of the derivation, covariate effects can be included for both models with seasonality and tagging effects investigated. Method robustness is established via comparison with the Fabens, improved Fabens, James and a non-linear mixed-effects growth models, with the maximum likelihood method performing the best. The method is illustrated further with an application to blacklip abalone (*Haliotis rubra*) for which a strong growth-retarding tagging effect that persisted for several months was detected.

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1. Introduction

Knowledge of how an aquatic species grows is fundamental to the stock assessment process. Growth, like other processes, is individual in nature and depends on many covariates such as seasonality, food availability, sex, among others. Growth models such as the von Bertalanffy growth model (VBGM) are often used to describe the mean growth of the population, however the growth process can be better understood by incorporating individuality and covariates into the model.

One of the difficulties with growth modelling is that the direct ageing of an aquatic species is often not possible. To solve this problem, fisheries rely on tag-recapture data to estimate the unknown parameters of a hypothesised representative model; for instance, the VBGM with parameters (k, μ_∞). Determining adequate estimates of growth parameters can be a complex problem when individual variability is considered (Wang et al., 1995; Wang and Die, 1996; Laslett et al., 2002). Many methods have been developed to account for the complexity of individual variability. James

(1991) provided a method for estimating the parameters of the VBGM via estimating functions that are unbiased, consistent and asymptotically normal. Wang et al. (1995) developed a maximum likelihood method (ML method) that accounted for individual variability in asymptotic length (L_∞) and the age at tagging (A) using distribution theory. Laslett et al. (2002) extended this idea by developing a flexible ML method for general growth curves with less restrictive assumptions, but again only for single-recapture data.

For many aquatic species multiple recapture data can be acquired. Solving for the growth parameters of a particular growth model using multiple-recapture data has either not been explored or is not easy to generalise mathematically. For instance, James (1991) explored multiple recaptures and found that the method for constructing the estimating functions for more than two recaptures, as well as unequal recaptures, was not clear. The method of Wang et al. (1995) requires, mathematically, the use of a single recapture to derive the likelihood function and thus is constrained to single-recapture analyses. Laslett et al. (2002) used different growth functions under a maximum likelihood routine, but only with a single recapture. Given that many tagging studies often include multiple recaptures, it makes sense to take advantage of these extra data. The inclusion of multiple recaptures should in theory improve growth estimates, because it allows for a better characterisation of each individuals growth trajectory by giving a greater number of growth snapshots; which is particularly important when individual variability is being modelled. More recaptures

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allow covariates such as seasonal growth to be modelled better because we have information across more seasons.

This paper derives a ML method to estimate growth parameters for general curves from simulated multiple recapture data; then applies it to a study of blacklip abalone (*Haliotis rubra*). The method rests on the ideas of distribution theory and requires the numerical integration of the joint distribution function for each individual. Individual variability in L_∞ and age at capture are taken into consideration, and given that the method is based on distribution theory the method should be asymptotically unbiased. Day and Fleming (1992) noted that not only average growth parameters but also the variation in these parameters must be known before reliable management models can be built for abalone species. It is clear from laboratory experiments that some variation in growth rates is endogenous for abalone species. Momma (1980) demonstrated than juvenile abalone of different ages, but the same sizes, maintained the same relative growth rates. Morse (1984) suggested that variability in growth among abalone siblings was a result of variation in growth hormone production. In the field chance differences between individuals in food supply and other environmental factors are likely; with variability at least in part dependent on the quality and quantity of algal food (Day and Fleming, 1992). Thus individual variability in abalone species is high, with both endogenous and exogenous factors playing a role. One of the key conclusions of Day and Fleming (1992) was that more attention needs to be paid to inherent variation between individuals in growth.

For abalone it has been conjectured that juvenile abalone do not follow a VBGM (Poore, 1972; Koike et al., 1979; Prince et al., 1988). There are many potential solutions to this problem; for instance, to model the juvenile component with a separate (linear) model, exclude the data that do not follow a VBGM, or use a different growth model. To keep the model continuous the latter two approaches are investigated here, with the Gompertz model used as an alternative. The Gompertz model has some precedence in the literature when modelling growth of blacklip abalone, and data analysis also suggests it is a reasonable choice (Troynikov et al., 1998; Helidoniotis et al., 2011). For *H. rubra* both Helidoniotis and Haddon (2012), and Prince et al. (1988) established that growth for juvenile abalone (those <80 mm) is best described by using a linear model. Prince et al. (1988) also established that once adulthood is reached then the VBGM models growth well. The straight-line growth observed for the smaller size classes of abalone has been observed or hypothesised for haliotids in a number of other studies such as Poore (1972), Koike et al. (1979), and Prince et al. (1988). However, Shepherd and Hearn (1983) observed early growth of haliotids to be non-linear. The use of the Gompertz model is explored, and covariates are introduced via a modification of the model presented in Jackson and Wang (1998).

Covariates can be included into the growth model to account for their effects. Gamito (1998) concluded that for long-lived fish the VBGM adjusted for seasonal growth is preferable to the logistic or Gompertz models. Day and Fleming (1992) noted that seasonal variation is very common in abalone species but underlying causes are usually confounded, and highlighted that food availability, gonad maturation (Sakai, 1962), and temperature (Chen, 1984) play important roles in seasonal variability. It has been shown for juvenile blacklip abalone that there is a strong seasonal effect, and its inclusion improved the model fit (Helidoniotis and Haddon, 2012). It is also conjectured that blacklip abalone from the Tasmanian (Australia) fishery could experience periods of no growth in the winter months. It is hypothesised that the tagging process has an effect on the growth of blacklip abalone. Xiao (1994) remarked that the most practical way to account for the effect of tagging is to quantify tagging effects concurrently with growth parameters. Wang (1998) used the generalised VBGM framework

Table 1

Summary of tag-recapture data for blacklip abalone. The variable L_j represents length at recapture j (mm), and T_j time at liberty between measurements L_{j-1} and L_j (years).

	Mean	SD	Range	Frequency
L_1	129	23.9	(26, 169)	1400
L_2	137	20.6	(34, 180)	1400
L_3	138	19.9	(40, 177)	383
L_4	142	17.1	(73, 165)	51
L_5	146	4.68	(139, 151)	9
L_6	140		(140, 140)	1
T_1	1.28	1.22	(0.00274, 6.99)	1400
T_2	1.91	1.41	(0.148, 7.45)	383
T_3	2.62	1.53	(0.441, 6.25)	51
T_4	3.73	1.81	(1.40, 6.31)	9
T_5	6.53		(6.53, 6.53)	1

to quantify the time taken to recover from tagging using a link function. The function represents a recuperation curve, and models a smooth transition to normal growth rather than the step-like function of Xiao (1994). Studies of abalone conclude that the handling process affects growth. Sakai (1962), Forster (1967) and Poore (1972) all reported growth marks on the shells of previously examined abalone. Tag type plays an important role too: wire tags threaded between the respiratory pores reduced growth in *H. rubra* (McShane et al., 1988; Harrison and Grant, 1971). If tagging is not modelled then the growth estimates are likely to be biased if this is not taken into consideration. We will investigate growth recovery after tagging of a population of blacklip abalone using the ML method under both the VBGM and Gompertz model. The principal aim of this paper is to present a ML method that uses multiple recaptures to model the effects of covariates (such as tagging) on growth for general growth curves.

2. Materials and methods

2.1. Data

To illustrate the method, multiple tag-recapture data from blacklip abalone were analysed. The tag-recapture data set for blacklip abalone, *H. rubra*, was gathered from a shallow study site at George III Rock, in southern Tasmania, Australia. The mark-recapture study included more than 1400 individuals with recapture frequency ranging from 1 to 5. Letting L_1 to L_6 be the lengths of individuals at each recapture, and T be the time at liberty, the data are summarised in Table 1. The data exhibited significant negative growth; therefore, a cutoff of −10 mm was chosen to be reasonable to retain a sufficient error structure; all those less than this cutoff were removed from the data. The method models measurement error and thus the inclusion of significant negative growth will not lead to biased results. Only 0.5% of the data exhibited negative growth less than −4 mm and thus these data do not dominate. Capture times were also summarised to determine if seasonality could be accurately modelled. Over the ten years that the data were gathered there appears to be a sufficient distribution of times to attempt to model seasonality.

Abalone were tagged with laminated numbered disc tags, secured by nylon rivet inserted into one of the respiratory pores, as described by Prince (1991). An advantage of this tagging method over others (external shell tags secured with epoxy glue, twisted-wire attachment through two adjacent respiratory pores) is that tags can be applied to abalone underwater Prince (1991), thereby minimising disturbance and stress, and consequent effects on survival and growth. In practice, however, tagging abalone underwater in the present study proved to be prohibitively time-consuming, especially at depths where no-decompression diving intervals are