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Research Article

Analysis of seasonal growth through the application of a multiple linear regression model on data from tag-and-recapture experiments

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Abstract

When the Brody coefficient K is subject to temporal variation, data from tag-and-recapture experiments permit analysis of seasonal growth. Temporal values for K can be estimated without using a pre-determined oscillating function and the impact of seasonality on annual growth can be analyzed more realistically. The method is applicable to intra-annual intervals of single or multiple cohorts.

Keywords: Fisheries; Population dynamics; Seasonal growth; Tagging experiments; Multiple linear regression.

Introduction

Most published methods for fitting the von Bertalanffy growth function (VBGF) where seasonality in growth is evident require an additional mathematical assumption as to how growth varies throughout the year. These methods generally apply to size-at-age data and are considered standard tools, such as the PAULY-GASCHÜTZ (1979) model and its modification by HOENIG & CHOUDARY HANUMARA (1982), and independently by SOMERS (1988). More elaborated techniques have been devised to improve the performance of seasonal VBGF fittings for data from tagging experiments (FRANCIS 1988), or size-at-age data (PAULY *et al.* 1992). All such models approximate the seasonal variation of the Brody coefficient **K** by means of pre-set periodic functions.

This study focuses on data from tagging experiments and suggests a method for fitting the VBGF in situations where the Brody coefficient **K** - and hence length increments - are subjected to temporal variations which do not necessarily correspond to a sinusoidal function. Rather than 'enriching' the VBGF with such an add-on function approximating seasonal variation in **K**, this method determines the seasonal fluctuation of **K** over time through a multiple linear regression procedure. This is based on two assumptions regarding **K** and $\mathbf{L_\infty}$ as well as a number of easily proven properties of the VBGF.

The method consists of two procedures. The first procedure - the focus of this study - optimizes the thirteen parameters of the model which are $\mathbf{L_\infty}$ and twelve monthly **K's.** The second procedure makes use of the estimated parameters and provides some additional information permitting some more insight into population growth.

Supplementary methodological notes are included in the last section (Theory).

Method

The method operates under two basic assumptions:

i) Fish growth follows the VBGF but is subject to monthly variations in **K**. These may cause fish to gain length in one month or show no increment in another (case when **K** is zero), or even to "statistically shrink" (**K**<0). **K** is the only parameter controlling the direction of increment within a month; this means that theoretical growth cannot be zero or negative when **K** is positive.

ii) As age increases, fish length approaches an asymptotic value $\mathbf{L_x}$ which is uniform and independent of the impact of seasonality on the growth pattern.

Notation and basic relationships

The following notation is used for tagging data of an individual:

- $\mathbf{D_a}$ and $\mathbf{D_b}$ are the dates of tagging and recapture respectively.
- $\mathbf{t_a}$ and $\mathbf{t_b}$ are the estimated ages at tagging and recapture respectively.
- **La** is the length at tagging and $\mathbf{L_b}$ is the length at recapture.
- $\mathbf{\Delta t}$ is the time lapsed between tagging and recapture and is expressed in years. $\mathbf{\Delta t}$ can be calculated on the basis of $\mathbf{D_a}$ and $\mathbf{D_b}$ when these are both known. Alternatively, when $\mathbf{\Delta t}$ is known then only one of the $\mathbf{D_a}$ or $\mathbf{D_b}$ need be indicated in the input dataset.
- $\mathbf{m_0}$ is the starting month containing point $\mathbf{t_0}$ (age at which length is zero – see equation (9)). Knowledge of $\mathbf{m_0}$ is a requisite for determining the starting point of a seasonal growth curve. Its role is analogous to that of parameter $\mathbf{t_s}$ used in sinusoidal models[2] that describe seasonal growth.

The method is based on some specific properties of the classical VB model. Most of these are self-evident; others are examined in more detail in Theory.

VBGF properties used by the presented method:

Property 1. If the asymptotic length $\mathbf{L_\infty}$ is uniform and season-independent and the growth rate **K** is constant in the interval $[\mathbf{D_a}, \mathbf{D_b}]$ we can write:

$$\mathbf{L_b = L_a + (L_\infty - L_a)(1 - e^{-K\Delta t})} \qquad (1)$$

This property derives from assumption (ii) given above. A more detailed discussion is given in Theory.

Property 2. It can be proved by induction (see Theory) that if the interval $\mathbf{\Delta t}$ in (1) consists of smaller intervals $\mathbf{\Delta t_i}$ (i.e. months or fractions of months) in each of which a monthly growth rate $\mathbf{K_i}$ applies, we will have:

$$\mathbf{L_b = L_a + (L_\infty - L_a)(1 - e^{-\sum K_i \Delta t_i})} \qquad (2)$$

or its inverse form:

$$L_a = L_b - (L_\infty - L_b)(e^{\sum K_i \Delta t_i} - 1) \qquad (3)$$

Property 3. Property 2 and expressions (1), (2) and (3) reveal that the growth rate **K** in (1) is the compound mean of all monthly growth rates occurring between the two dates D_a and D_b :

$$K = \frac{1}{\Delta t} \sum K_i \Delta t_i \qquad (4)$$

Property 4. When the start length L_a in (1) is the length L_0 at age zero, then any length L_t at age **t** will be:

$$L_t = L_0 + (L_\infty - L_0)(1 - e^{-K_{0,t}t}) \qquad (5)$$

$K_{0,t}$ being this time the running average of the monthly growth rates occurring between **0** and **t**. Expression (5) is the seasonal version of the original VON BERTALANFFY (1938) equation.

Property 5. By considering expressions (2) and (4) we can write:

$$-\ln \frac{L_\infty - L_b}{L_\infty - L_a} = K\Delta t = \sum K_i \Delta t_i \qquad (6)$$

Property 6. When each of the time intervals in (4) is equal to 1/12 years then any segment of twelve successive monthly **K's** will furnish the same arithmetic mean (or annual average):

$$K_A = (1/12) \sum_{j=1}^{12} K_j$$

Moreover the running average $K_{0,t}$ in (5) will oscillate about K_A (Fig. 1). It can easily be proved that the annual average coincides with the annual growth rate resulting from the classical VB model when lengths are measured at regular annual intervals and seasonal variations of **K** are ignored (see Theory). Such cases of comparability, however, can only be found in size-at-age data and not in tagging experiments where the time at liberty is expressed in variable time intervals. This point is further analyzed in Discussion.

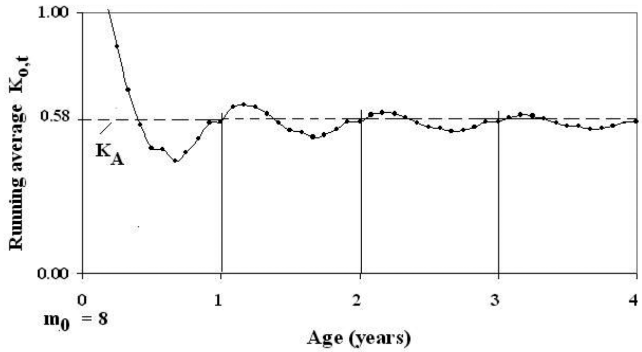

Fig. 1: Oscillation of the running average $K_{0,t}$ during four years of growth. The plot made use of the simulated data of the Example and the assumption that the starting month m_0 is 8. Note that $K_{0,t}$ is equal to K_A when ages are exact year multiples and that as age increases, K_A is the limit of $K_{0,t}$.

The two procedures of the presented method:

As mentioned in the Introduction the proposed method is applicable in situations where dates of tagging and recapture are available. The individuals are generally of different cohorts, and lengths may be measured over time intervals in which different growth rates apply. The method is implemented by means of two distinct procedures. The first procedure uses trial values of $\mathbf{L_\infty}$ to optimize the parameters of a multiple linear regression model. The second procedure is a computational supplement to the first: making use of the results of the optimization approach to estimate the ages of individuals at tagging and recapture. VB growth curves are created illustrating both input and theoretical lengths (Figs 2 and 3).

First procedure: Optimization of growth parameters by means of a multiple linear regression model

Measured lengths at tagging and recapture of individuals are contained in a dataset of **N** tag-and-recapture records. If the dates of tagging and recapture are known the right term of expression (6) (which can involve a variable number of monthly periods or fractions of months), can always take the following standard form of twelve monthly elements:

$$-\ln \frac{L_\infty - L_b}{L_\infty - L_a} = Y = \sum_{j=1}^{12} K_j X_j \qquad (7)$$

where:

- $\mathbf{L_\infty}$ is a trial value of the uniform asymptotic length;
- The twelve coefficients $\mathbf{K_1, \ldots, K_{12}}$ represent monthly **K** values to be estimated.
- The values of the twelve independent variables $\mathbf{X_1, \ldots, X_{12}}$ are the frequencies with which months appear in the time lapsed between tag and recapture.

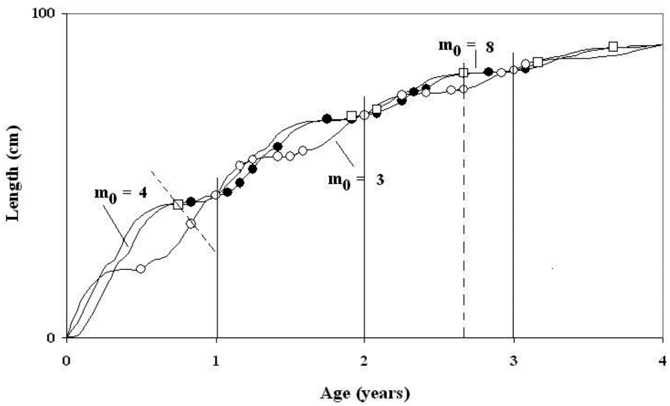

Fig. 2: Plotting of input data and theoretical lengths resulting from the simulated tagging data of the Example. There are three starting months equal to 3, 4, and 8 respectively, thus resulting in three different VB curves. Dotted lines indicate that for individuals with different starting months there can exist theoretical lengths that are smaller than those corresponding to earlier ages (first case), or that individuals may have different theoretical lengths although they are of the same age (second case).

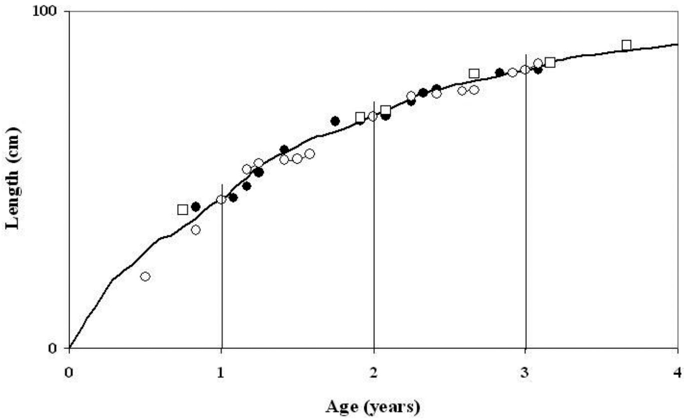

Fig. 3: Plot of a probabilistic seasonal curve generated from the input data and results of the Example. The curve converges to the same asymptotic length $L_\infty = 100$.

These values depend only on the input dates at tagging and recapture and are not affected by the trial values of $\mathbf{L_\infty}$. The monthly frequencies will be zeroes for months that do not fall between tag and recapture. For the others the frequencies will be fractions of a month or multiple months (see numerical Example).

By writing formula (7) for all **N** records we obtain a multiple linear regression matrix which can be processed by means of standard methods available in most computers[3]. For each trial $\mathbf{L_\infty}$ there will be twelve estimates for the monthly **K's** and a goodness-of-fit indicator $\mathbf{R^2}$. Optimal $\mathbf{L_\infty}$ and **K's** are those that maximize $\mathbf{R^2}$. Since the parameters that take part in the optimization process are $\mathbf{L_\infty}$ and the twelve monthly **K's,** it follows that when dealing with tagging data the degrees of freedom of the model are **N** – 13.

<u>Second procedure: Supplementary outputs based on the results of the optimization approach</u>

This procedure exploits further the results from the multiple linear regression model and produces the following two sets of supplementary outputs: (a) estimated absolute ages of individuals at tagging and recapture and, (b) estimated starting months $\mathbf{m_0}$ for all individuals (refer to Notation for an explanation of $\mathbf{m_0}$). A detailed description of the related algorithm is given in Theory.

VB plots

In tagging experiments, individuals of the same age may have different predicted lengths since their seasonal growth curves may have different starting months $\mathbf{m_0}$ (Notation earlier and examples in Fig. 2). This means that there will be as many VB curves as there are different starting months $\mathbf{m_0}$ in the samples. However according to Property 6 individuals with ages that are exact multiples of 12 months will have the same predicted lengths irrespective of their respective $\mathbf{m_0}$.

Multiple VB curves may be mathematically exact but are not very convenient for practical use. An alternative approach is to set-up a probabilistic VB curve in which for a given age there will correspond only one predicted length. This length will be the weighted mean of all lengths predicted by each of the VB curves discussed above. The weighting factors will be the relative frequencies of the starting months $\mathbf{m_0}$ in the samples.

For instance in the 22 tagging records of Example, starting month $\mathbf{m_0} = 8$ appears ten times, $\mathbf{m_0} = 3$ nine times and $\mathbf{m_0} = 4$ three times (right column of Table 1). Assuming that the relative frequencies 10/22, 9/22 and 3/22 are representative of the individuals in the population, a probabilistic VB curve can be constructed in which predicted lengths are calculated by first multiplying the theoretical lengths of each curve by their respective relative frequency (i.e. 10/22, 9/22, or 3/22) and adding them together (Fig. 3).

Note that probabilistic VB curves will have an asymptotic limit identical to the $\mathbf{L_\infty}$ estimated earlier, and that in general they will be more realistic than those resulting from non-seasonal approaches (see related paragraph in Discussion).

Example: Simulated tagging data

In this example the multiple linear regression approach was applied to 22 records of simulated tagging data generated with $\mathbf{L_\infty} = 100$ cm and twelve monthly **K** values shown at the bottom of Table 1. The simulated tagging records were generated with the following starting month frequencies: 10 records with $\mathbf{m_0} = 8$, 9 records with $\mathbf{m_0} = 3$ and 3 records with $\mathbf{m_0} = 4$. Tag and recapture dates $\mathbf{D_a}$, $\mathbf{D_b}$ were deliberately set to the starting and ending day of a month in order to facilitate visualization of the month frequencies that were used as values of the twelve independent variables $\mathbf{X_1, \ldots, X_{12}}$ in equation (7). For instance in the second record of Table 1 the time lapsed between 1 June 2007 and 30 June 2008 is expressed as 2x(1/12) years for June and 1x(1/12) years for all other months. Had the tagging date been 20 June 2007 the frequency of June would have been (0.333 + 1)x(1/12). In order to express $\mathbf{X_1, \ldots ,X_{12}}$ as integral numbers, column **Y** was multiplied by 12.

Table 1 also illustrates the input matrix (column **Y** and the twelve independent variables $\mathbf{X_1, \ldots , X_{12}}$) that was used by the LINEST linear regression procedure of MS-Excel at the trial value $\mathbf{L_\infty} = 100$.

Application of the first procedure: Optimization process

A simple MS-Excel macro was prepared to generate trial $\mathbf{L_\infty}$ values in the range of 90 – 110 cm using increments of 1 cm. Each trial value of $\mathbf{L_\infty}$ generated 22 values of the dependent variable **Y** by means of formula (7). The LINEST procedure of the MS-Excel was then applied to the input matrix consisting of column **Y** and the twelve columns representing the independent variables (i.e. month frequencies) $\mathbf{X_1, \ldots , X_{12}}$. Each run of LINEST resulted in twelve estimates for **K's** and a goodness-of-fit $\mathbf{R^2}$. Optimal $\mathbf{L_\infty}$ and **K's** were those for which $\mathbf{R^2} = 1$. As expected these optima coincided with the values of $\mathbf{L_\infty}$ and **K's** that were used to simulate the lengths at tagging and recapture.

Application of the second procedure: Calculation of additional parameters

On the basis of the optimized parameters $\mathbf{L_\infty}$ and the twelve monthly **K's** the second procedure of the method was applied in order to calculate for each individual the starting month $\mathbf{m_0}$ and the absolute ages at tagging and recapture respectively

Table 1

Input matrix and optimal results (bottom part) of the multiple linear regression corresponding to the trial value $L_\infty = 100$. Use was made of the standard procedure LINEST of MS Excel. To be noted that column Y was multiplied by 12 in order to provide a better visualization of the month frequencies (i.e. independent variables) $X_1, \dots, X_{12}$.. The estimated starting months m_0 of the individuals are shown on the right-hand column

#	Tag date	Recapt. date	Tag. length	Recapt. length	Dep. Var.	Independent variables $X_1, \dots, X_{12}$												Resulting starting months
	D_a	D_b	L_a	L_b	Y x 12	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	m_0
1	01/08/2008	31/10/2008	76.9	81.4	2.600	0	0	0	0	0	0	0	1	1	1	0	0	3
2	01/06/2007	30/06/2008	52.0	75.7	8.160	1	1	1	1	1	2	1	1	1	1	1	1	3
3	01/12/2007	31/01/2008	67.3	67.5	0.060	1	0	0	0	0	0	0	0	0	0	0	1	3
4	01/01/2007	28/02/2007	41.8	44.0	0.460	1	1	0	0	0	0	0	0	0	0	0	0	3
5	01/03/2008	31/05/2008	68.7	73.1	1.850	0	0	1	1	1	0	0	0	0	0	0	0	3
6	01/04/2007	30/04/2007	44.7	47.8	0.700	0	0	0	1	0	0	0	0	0	0	0	0	3
7	01/01/2008	31/03/2009	81.8	82.7	0.610	1	1	1	0	0	0	0	0	0	0	0	0	3
8	01/08/2007	31/01/2009	58.7	81.8	9.820	2	1	1	1	1	1	1	2	2	2	2	2	3
9	01/03/2007	31/03/2008	44.0	69.0	7.110	1	1	2	1	1	1	1	1	1	1	1	1	3
10	01/02/2007	29/02/2008	41.1	68.3	7.410	1	2	1	1	1	1	1	1	1	1	1	1	4
11	01/06/2009	30/11/2009	84.8	89.6	4.600	0	0	0	0	0	1	1	1	1	1	1	0	4
12	01/05/2008	31/01/2009	70.4	81.5	5.660	1	0	0	0	1	1	1	1	1	1	1	1	4
13	01/02/2007	29/02/2008	21.2	57.5	7.410	1	2	1	1	1	1	1	1	1	1	1	1	8
14	01/11/2007	28/02/2009	54.9	76.2	7.670	2	2	1	1	1	1	1	1	1	1	2	2	8
15	01/03/2008	31/07/2009	57.5	82.4	10.610	1	1	2	2	2	2	2	1	1	1	1	1	8
16	01/08/2007	30/09/2007	44.0	53.0	2.100	0	0	0	0	0	0	0	1	1	0	0	0	8
17	01/01/2008	31/12/2008	55.8	75.3	6.960	1	1	1	1	1	1	1	1	1	1	1	1	8
18	01/08/2008	31/10/2008	68.7	74.8	2.600	0	0	0	0	0	0	0	1	1	1	0	0	8
19	01/08/2009	31/08/2009	82.4	84.3	1.300	0	0	0	0	0	0	0	1	0	0	0	0	8
20	01/06/2007	30/06/2009	34.9	81.5	15.120	2	2	2	2	2	3	2	2	2	2	2	2	8
21	01/02/2008	31/07/2008	55.9	68.7	4.100	0	1	1	1	1	1	1	0	0	0	0	0	8
22	01/01/2008	31/03/2009	55.8	76.5	7.570	2	2	2	1	1	1	1	1	1	1	1	1	8
						Resulting monthly K's												
						0.01	0.45	0.15	0.7	1	1.2	0.6	1.3	0.8	0.5	0.2	0.05	
						Goodness of fit $R^2 = 1$						Annual average $K_A = 0.58$ /year						

(see Method earlier). This complementary approach permitted the construction of three VB curves and of a probabilistic VB curve as shown in Figures 2 and 3 respectively.

Impact of seasonality on the Brody coefficient K

Figures 1 and 2 reveal that the impact of seasonality on growth is more visible in early ages and that this impact progressively diminishes with age. This is explained by recalling formula (5). From the way $\mathbf{K_{o,t}}$ is formulated it is easy to prove (see Theory) that: (i) $\mathbf{K_{o,t}}$ oscillates about the annual average $\mathbf{K_A}$ and; (ii) $\mathbf{K_A}$ is the limit of $\mathbf{K_{o,t}}$ as the oscillation diminishes with age. Figure 1 illustrates an example of the oscillation of $\mathbf{K_{o,t}}$ based on the twelve monthly **K's** estimated in the Example. The first $\mathbf{K_{o,t}}$ of the curve is the monthly **K** corresponding to starting month $\mathbf{m_0} = 8$. It is recalled that in the Example the annual average $\mathbf{K_A}$ is 0.58.

Discussion

On the basis of the theory and example presented we may conclude that in the case of data from tagging experiments seasonality of growth can be modelled without making assumptions as to its form. A glance at Figures 1 and 2 shows that the numerical properties of the running average $\mathbf{K_{o,t}}$ suffice to explain the impact of monthly variations in **K** without incorporating an oscillating function into the VBGF.

From the viewpoint of applicability, the present study stresses that if sufficient and reasonably accurate samples of tagging data are available, the resulting estimates of $\mathbf{L_\infty}$ and monthly **K's** can further be exploited to offer a better insight into the aspects of population growth. To be noted that analysis of tagging data seems to be less susceptible to statistical noise than data on size-at-age. Measuring errors apart (since they can affect both tagging and size-at-age), the case of an individual showing zero or negative growth during the time at liberty is a case that needs to be considered. In size-at-ages however such a case may be accidental and caused by the inclusion of individuals with different starting months $\mathbf{m_0}$ (Fig. 2).

A possible risk in the optimization of $\mathbf{L_\infty}$ is the presence of old individuals in the samples. The logarithmic term in equation (7) must not contain zero or negative items; this restriction limits the trial values of $\mathbf{L_\infty}$.

The authors also examined situations where non-seasonal models apply to tag-and-recapture data in which seasonality may be evident. Figure 4 illustrates two cases in each of which the non-seasonal VONBIT procedure for tagging data was applied (STAMATOPOULOS & CADDY, 1989). In the first case use was made of the simulated data of the Example, while the second case used actual data for male *Panulirus homarus* from the west coast of India (MOHAMED & GEORGE , 1971). Both plots show a rather high dispersion of points which in the case of simulated data (see Example) is known to be totally due to seasonality, while in the second case it could be interpreted as statistical noise. This fact suggests that when non-seasonal tagging applications show similar plots, point dispersion might be partially reduced if the model in use also takes into consideration the effect of seasonality on growth. However, as already mentioned in Method, a prerequisite for such an approach would be the inclusion of tagging and recapture dates into the input dataset.

As a last remark the authors wish to point out that from the methodological view-

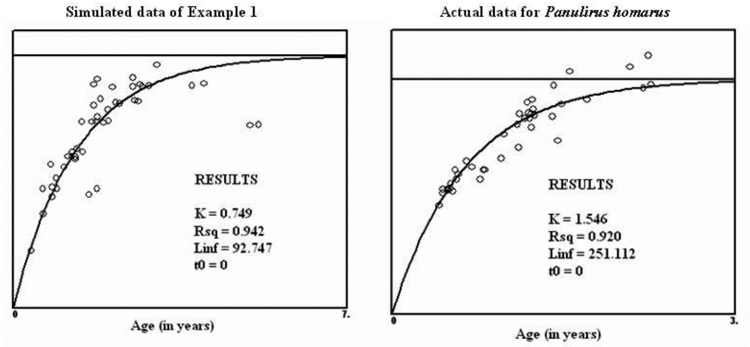

Fig. 4: Example of the application of non-seasonal procedures to tagging data. In the first plot the simulated data of the Example were used. The second plot was obtained from tag and recapture experiments of MOHAMED & GEORGE (1971) for male *Panulirus homarus.*

point the present study mainly deals with conceptual rather than statistical aspects. The reason is that if the idea of focusing on the natural oscillation of **K** is accepted, then the authors do not exclude the possibility that optimizing the seasonal parameters $\mathbf{L_\infty}$ and monthly **K's** can be achieved by approaches that are statistically more elegant and computationally more robust. The choice of multiple linear regression was driven by the fact that the latter is convenient, known to most users and readily available as a standard statistical instrument.

A simple Excel-based program can be provided to users who wish to process and analyze seasonal tagging data.

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Theory

This section provides guidance for the derivation of some of the properties and approaches presented in Method.

Proof of Property 1

We first recall the two classical VB formulae:

$$\mathbf{L_t = L_0 + (L_\infty - L_0)(1 - e^{-Kt})} \qquad (8)$$

$$\mathbf{L_t = L_\infty [1 - e^{-K(t - t_0)}]} \qquad (9)$$

which apply when $\mathbf{K}$ is assumed to be uniform in age intervals [0 , $\mathbf{t}$] and [$\mathbf{t_0}$, t] respectively. Expression (8) is the original von BERTALANFFY (1938) equation while expression (9) is its transformed version by BEVERTON & HOLT (1957). The proof of Property 1 derives from expression (8). Let us consider an individual with two theoretical lengths: $\mathbf{L_a}$ at tagging date $\mathbf{D_a}$ and $\mathbf{L_b}$ at recapture date $\mathbf{D_b = D_a + \Delta t}$. The growth rate $\mathbf{K}$ is assumed to be uniform in the interval [$\mathbf{D_a}$, $\mathbf{D_b}$]. We then set-up tagging and recapture ages $\mathbf{t_a} = 0$ and $\mathbf{t_b} = \mathbf{\Delta t}$ respectively. Using the above settings we can write (8) with $\mathbf{L_a}$ playing the role of $\mathbf{L_0}$ and $\mathbf{L_b}$ that of $\mathbf{L_t}$, thus obtaining:

$$\mathbf{L_b = L_0 + (L_\infty - L_0)(1 - e^{-Kt_b}) =}$$

$$\mathbf{= L_a + (L_\infty - L_a)(1 - e^{-K\Delta t})}$$

, hence Property 1.

Proof of Property 2

The second proof concerns the case where the interval $\mathbf{\Delta t}$ in expression (1) is made up of $\mathbf{n}$ smaller intervals $\mathbf{\Delta t_i}$ (i=1,2,...,$\mathbf{n}$), in each of which different growth rates $\mathbf{K_i}$ apply. It will be proved by induction that in such a case we can write:

$$\mathbf{L_b = L_0 + (L_\infty - L_0)(1 - e^{-\sum_1^n K_i \Delta t_i})} \qquad (10)$$

We first observe that the property holds for $\mathbf{n}=1$ since in the case of only one time interval $\Delta\mathbf{t}$ expression (1) is valid. Next it will be shown that if (10) is true for $\mathbf{n}$ intervals it will also be true for $\mathbf{n+1}$ intervals, in which case the property will be fully proved. Since (10) is assumed to be true for $\mathbf{n}$ intervals, length $\mathbf{L}$ at the end of interval $\Delta\mathbf{t_n}$ will be given by:

$$\mathbf{L = L_a + (L_\infty - L_a)(1 - e^{-\sum_{j=1}^{n} K_i \Delta t_i})} \qquad (11)$$

On the other hand by applying formula (1) to lengths $\mathbf{L}$ and $\mathbf{L_b}$ in the interval $\Delta\mathbf{t_{n+1}}$ we will have:

$$\mathbf{L_b = L + (L_\infty - L)(1 - e^{-K_{n+1}\Delta t_{n+1}})} \qquad (12)$$

By substituting in (12) the expression for $\mathbf{L}$ in (11) we obtain:

$$\mathbf{L_b = L_a + (L_\infty - L_a)(1 - e^{-\sum_{j=1}^{n+1} K_i \Delta t_i})}$$

, hence Property 2.

Proof of property 6

Here we shall prove that if $\mathbf{K_A}$ is the annual average of twelve monthly $\mathbf{K's}$ then the running average $\mathbf{K_{0,t}}$ used in expression (5) will: (i) oscillate about $\mathbf{K_A}$ and, (ii) will have $\mathbf{K_A}$ for its limit as age increases. Without loss of generality we make the assumption that the period between age $\mathbf{t_0}$ at which length is zero and any age $\mathbf{t}$ contains $\mathbf{n}$ monthly intervals. In this case equation (4) takes the simpler form:

$$\mathbf{K_{0,t} = \frac{1}{n} \sum K_i} \quad .$$

If the period $[\mathbf{t_0}, \mathbf{t}]$ contains exactly $\mathbf{y}$ years it follows that $\mathbf{n}$ will be an exact multiple of 12 and last equation becomes:

$$\mathbf{K_{0,t} = \frac{1}{12y} 12yK_A = K_A} \quad .$$

In other words when the running average $\mathbf{K_{0,t}}$ is calculated over 12 monthly periods of whatever order its value is always equal to the annual average $\mathbf{K_A}$ (Fig. 1). This also means that even when seasonality in growth is evident, the non-seasonal VBGF is still valid provided that lengths are measured at regular annual intervals. In such a case the resulting $\mathbf{K}$ will be the annual average $\mathbf{K_A}$.

We next consider the case when the period $[0, \mathbf{t}]$ contains $\mathbf{y}$ years $(\mathbf{y \geq 1})$ and $\mathbf{p}$ months $(0<\mathbf{p}<12)$. Equation for $\mathbf{K_{0,t}}$ becomes:

$$\mathbf{K_{0,t} = \frac{1}{(12y+p)} (12yK_A + \sum_{i=1}^{p} K_i) =}$$

$$\mathbf{= \frac{1}{(1+p/12y)} [K_A + (\sum_{i=1}^{p} K_i) / 12y]}$$

As $\mathbf{y}$ increases the terms $\mathbf{(1 + p/12y)}$ and

$$\mathbf{(\sum_{i=1}^{p} K_i) / 12y}$$

tend to become 1 and 0 respectively; this in turn means that as age increases the running average $\mathbf{K_{0,t}}$ has for its a limit the annual average $\mathbf{K_A}$.

Algorithm for estimating ages and starting months $\mathbf{m_0}$ for individuals

Let us assume that optimal values for $\mathbf{L_\infty}$ and monthly $\mathbf{K's}$ have been computed at an earlier stage. We then consider an individual with lengths $\mathbf{L_a}$ and $\mathbf{L_b}$ at tagging and recapture respectively. First task will be the estimation of $\mathbf{L_0}$ at a relative age $\mathbf{t} = 0$. We start by assigning a relative age of 1/12 to the beginning of the month containing tagging date $\mathbf{D_a}$. In this manner the relative age $\mathbf{t_a}$ at $\mathbf{D_a}$ is known and so is $\mathbf{t_b} = \mathbf{t_a} + \mathbf{\Delta t}$. Evidently relative age 0 will be at the beginning of the preceding interval (Fig. 5). On the basis of the above observations the two growth paths in the intervals $[0 , \mathbf{t_a}]$ and $[0 , \mathbf{t_b}]$ are known and we can write formula (5) twice:

$$\mathbf{L_b = L_0 + (L_\infty - L_0)(1 - e^{-K_{0,t_b}t_b})} \quad (13)$$

$$\mathbf{L_b = L_0 + (L_\infty - L_0)(1 - e^{-K_{0,t_b}t_b})} \quad (14)$$

If $\mathbf{L_a = L_b}$ (case of zero growth) length $\mathbf{L_0}$ can be estimated from either (13) or (14).

If $\mathbf{L_a}$ # $\mathbf{L_b}$ we can eliminate the term $(\mathbf{L_\infty - L_0})$ between (13) and (14) to obtain:

$$\mathbf{L_0 = L_a - (L_b - L_a)\frac{1 - e^{-K_{0,t_a}t_a}}{e^{-K_{0,t_a}t_a} - e^{-K_{0,t_b}t_b}}} \quad (15)$$

Starting with the newly estimated $\mathbf{L_0}$ we apply a repeating process in which formula (3) calculates lengths in reverse order. For instance by setting $\mathbf{L_b = L_0}$ in (3) we can calculate $\mathbf{L_a}$ at age 0-1/12. We then set $\mathbf{L_b = L_a}$ and re-calculate $\mathbf{L_a}$ at age 0-2/12. The process is repeated until $\mathbf{L_a}$ has become zero or negative. Meanwhile we keep track of all successive alterations of ages and months as shown in Figure 5.

If the final $\mathbf{L_a}$ is zero then the relative age at the beginning of the current interval will itself be the VB parameter $\mathbf{t_0}$. If $\mathbf{L_a}$ is negative (see example in Fig. 5) then parameter $\mathbf{t_0}$ is given by VB formula (9).

With $\mathbf{t_0}$ estimated ages $\mathbf{t_a - t_0}$ and $\mathbf{t_b - t_0}$ will represent estimated absolute ages at tagging and recapture respectively for the individual under study.

By applying the above algorithm to all individuals in the input dataset we obtain a set of results containing estimated absolute ages at tagging and recapture as well as starting months $\mathbf{m_0}$. In this manner input and estimated data can be plotted as shown in Figures 2 and 3.

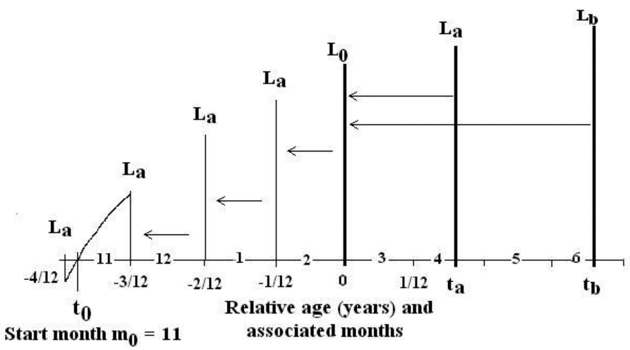

Fig. 5: Graphical representation of the numerical process for the estimation of starting month m_0 and absolute ages at tagging and recapture of an individual.