On a Seasonally Oscillating Growth Function

IAN F. SOMERS
Division of Fisheries Research, CSIRO Marine Laboratories
P.O. Box 120, Cleveland, Qld 4163, Australia

Introduction

There have been several papers describing the incorporation of seasonal oscillation into the standard von Bertalanffy growth function (Pitcher and Macdonald 1973; Cloern and Nichols 1978; Pauly and Gaschütz 1979). Of these, the seasonal growth model most commonly used in tropical fisheries is that of Pauly and Gaschütz, probably because of its availability as an option in the now widely used ELEFAN routines (Pauly and David, 1981). Recently, Appeldoorn (1987) described a modification of the Pauly and Gaschütz model for use with mark-recapture data. On reading the paper by Appeldoorn, I have formed the opinion that there may be some confusion creeping into the literature because of a basic flaw in the derivation of the Pauly and Gaschütz model.

Most workers who have modelled growth of fish will be familiar with the standard von Bertalanffy growth function

$$L_t = L_\infty \{1 - e^{-[K(t - t_0)]}\} \quad \ldots 1)$$

where L_t is the length at age t, t_0 the theoretical age when $L_t = 0$, L_∞ the asymptotic length and K, a growth constant.

The Pauly and Gaschütz model is virtually identical to the sine wave growth model described earlier by Pitcher and Macdonald (1973). In the Pitcher and Macdonald model (their equations 5 and 6), the growth constant K of equation 1 above was redefined as a sine function with a wave length of one year such that

$$L_t = L_\infty \{1 - e^{-[K(t - t_0) + C\sin 2\pi(t - t_s)]}\} \quad \ldots 2)$$

where C was a constant which indicated the magnitude of the oscillation and t(s) defined the beginning of the sine wave. In the Pauly and Gaschütz model, the constant C was redefined in relation to the constant K such that

$$L_t = L_\infty \{1 - e^{-[K(t - t_0) + (CK/2\pi)\sin 2\pi(t - t_s)]}\} \quad \ldots 3)$$

Pauly and Gaschütz argued that, in this form, the parameter C was more easily interpreted with respect to the amplitude of growth oscillations. To simplify the algebra, both of the above models (equations 2 and 3) can be reduced to the form

$$L_t = L_\infty \{1 - e^{-[K(t - t_0) + S(t)]}\} \quad \ldots 4)$$

In the case of Pauly and Gaschütz, $S(t) = (CK/2\pi) \sin 2\pi (t-t_s)$.

The flaw in both models arises in relation to the definition of t_0. Substitution of t_0 for t does not produce an L_t of 0, except when $S(t_0)$is equal to 0. $S(t_0)$ is equal to 0 if, and only if, t_0 equals t_s (or $t_s + N$, where N is an integer number of years). A more appropriate form for the model would be

$$L_t = L_\infty \{1 - e^{-[K(t - t_0) + S(t) - S(t_0)]}\} \quad \ldots 5)$$

which can be derived from the basic underlying principles as shown in Appendix 1.

Although, both Appeldoorn and Pauly and Gaschütz described the model of Cloern and Nichols (1978, equation 6) as being analogous to equation 4, it does not contain the same problem with t_o and is clearly analogous to equation 5. The main difference with the Cloern and Nichols model is that they redefine t_o as time of recruitment with size at t_o defined as the minimum size L_{min}.

What is the effect of S(to) in the tag-recapture growth model?

In the derivation of a form of the model which is suitable for tag-recapture data, both t_o and $S(t_o)$ are eliminated (Appendix 2).

$$I = (L_\infty - L_t)\ \{1 - e^{-[Kd - S(t) + S(t+d)]}\} \qquad \ldots 6)$$

where I is the growth increment, L_t the size at release and d the time at liberty.

It should be noted that this model would have been derived whether $S(t_o)$ was included in the original model or not. An example of this is the model used by Shepherd and Hearn (1983, equations 4 and 6) to model the seasonal growth of abalone. Their model is identical to equation 6 above, yet was derived from the Pitcher and Macdonald model. Consequently Appeldoorn's model, which was derived from that of Pauly and Gaschütz should also have been identical to equation 6. However, to add to the confusion, this was not the case, although the reason is because of an error in the Appeldoorn paper, rather than a peculiarity of the model. The right hand side of his equation 4 is equal to growth increment, not the length at recapture as indicated. I assume this was simply a typographical error (which is repeated in the author's equation 5), otherwise it would not have been possible to recover the parameter values of the simulated example 1.

The reason that the basic flaw in both the Pauly and Gaschütz and the Pitcher and Macdonald models has not been exposed earlier, considering their numerous applications, is probably because the additional term has little impact on the fitted values of the main parameter L_∞ and K. In fitting the revised model to the data given in example 1 of Pauly and Gaschütz (1979), there was no significant improvement in the fit and only the estimate of t_o was affected (9%).

Appendix 1
Derivation of a von Bertalanffy growth model, incorporating seasonal variation in growth

Let us assume that under constant temperature, the rate of growth (from equation 1) is

$$\frac{dL}{dt} \text{ proportional to } (L_\infty - L_t) \qquad \ldots 7)$$

Furthermore, let us suppose that, for any given size, the rate of growth is also dependent on the water temperature such that

$$\frac{dL}{dt} \text{ proportional to } (T^o - T^o_m) \qquad \ldots 8)$$

where $(T^o\text{-}T^o_m)$ is the difference between the temperature T^o and some critical minimum temperature T^o_m at which rate of growth is zero.

Let us also suppose the temperature over a year follows a sinusoidal pattern such that it can be described by

$$T^o = A \cos 2\pi(t - t_s) + B \qquad \ldots 9)$$

where t_s defines the time (in years) of the start of the cycle (and at which the T^o has a maximum (A + B)). Then

$$(T^o - T^o_m) = A\cos 2\pi(t - t_s) + B - T^o_m \qquad \ldots 10)$$

Thus, combining equations 7, 8 and 10 and reducing the constants to the simplest form, we obtain a model for the rate of growth under a seasonally oscillating temperature regime as

$$\frac{dL}{dt} = K(L_\infty - L_t)\,(C\cos 2\pi(t - t_s) + 1) \qquad \ldots 11)$$

On integrating, this becomes

$$L_t = L_\infty - e^{-[(KC/2\pi)\sin 2\pi(t - t_s) + Kt + D]} \qquad \ldots 12)$$

where D is a constant. To solve for D, we substitute $t = t_o$ and $L_t = 0$, from which

$$e^{-D} = L_\infty e^{[(KC/2\pi)\sin 2\pi(t_o - t_s) + Kt_o]} \qquad \ldots 13)$$

Thus equation 12 transforms to

$$L_t = L_\infty - e^{-[(KC/2\pi)\sin 2\pi(t - t_s) + KT]} L_\infty e^{[(KC/2\pi)\sin 2\pi(t_o - t_s) + Kt_o]} \qquad \ldots 14)$$

which can be reduced to the form

$$L_t = L_\infty \{1 - e^{-[K(t - t_o) + S(t) - S(t_o)]}\} \qquad \ldots 15)$$

where, as in equation 4, $S(t) = (CK/2\pi)\sin 2\pi\,(t - t_s)$.

Appendix 2
Derivation of a form of the seasonally oscillating von Bertalanffy growth function, suitable for tag-recapture data

After time at liberty d, the length attained L_{t+d} after release at length L_t will be

$$L_{t+d} = L_\infty \{1 - e^{-[K(t + d - t_o) + S(t + d) - S(t_o)]}\} \qquad \ldots 16)$$

Substituting $S(t+d) = S(t+d) + S(t) - S(t)$ in equation 16, we obtain

$$L_{t+d} = L_\infty - L_\infty \{e^{-[K(t - t_o) + S(t) - S(t_o)]} e^{-[Kd - S(t) + S(t + d)]}\} \qquad \ldots 17)$$

From equation 15,

$$L_\infty - L_t = L_\infty e^{-[K(t - t_o) + S(t) - S(t_o)]} \qquad \ldots 18)$$

Hence equation 17 can be reduced to

$$L_{t+d} = L_\infty - (L_\infty - L_t)\, e^{-[Kd - S(t) + S(t + d)]} \qquad \ldots 19)$$

or alternatively, the growth increment $I = (L_{t+d} - L_t)$ can be described by

$$I = (L_\infty - L_t)\, \{1 - e^{-[Kd - S(t) + S(t + d)]}\} \qquad \ldots 20)$$

References

Appeldoorn, R. 1987. Modification of a seasonally oscillating growth function for use with mark-recapture data. J. Cons. Int. Explor. Mer 43:194-198.

Cloern, J.E. and F.H. Nichols. 1978. A von Bertalanffy growth model with a seasonally varying coefficient. J. Fish. Res. Bd. Can. 35:1479-1482.

Shepherd, S.A. and W.S. Hearn. 1983. Studies on southern Australian abalone (Genus Haliotus). IV Growth of H. laevigata and H. ruber. Aust. J. Mar. Freshw. Res. 34:461-475.

Pauly, D. and N. David. 1981. ELEFAN I, a basic program for the objective extraction of growth parameters from length-frequency data. Meeeresforsch. 28(4):205-211.

Pauly, D. and G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. ICES CM 1979/G:24:26 p.

Pitcher, T.J. and P.D.M. Macdonald. 1973. Two models for seasonal growth in fishes. J. App. Ecol. 10:599-606.

Splitting Length Distributions into Peaks and the Clean Class Concept

HANS LASSEN
Danish Institute of Fisheries and Marine Research
Charlottenlund Slot, DK2920 Charlottenlund, Denmark

The problem which we shall address in this contribution is that of splitting a composite length sample into its component distributions, each of which should be identified as an age-group.

The splitting is often done using methods which require that only one age-group contribute to the length distribution in a certain length range. A length range where all fish have the same age is called a "clean class".

It is here assumed that the growth of fish follows some growth function, e.g., a von Bertalanffy curve and that, for a given age, the lengths around the growth curve are normally distributed.
The basic model is

$$n(L) = N_1 \frac{dL}{\sqrt{2\pi}\,\sigma_1} \exp\left[-\frac{1}{2}\left(\frac{L-\bar{L}_1}{\sigma_1}\right)^2\right] + N_2 \frac{dL}{\sqrt{2\pi}\,\sigma_2} \exp\left[-\frac{1}{2}\left(\frac{L-\bar{L}_2}{\sigma_2}\right)^2\right] + \ldots\ldots$$

for a total of K-terms, where

$n(L)$	:	the number of fish in length class 1 (midlength)
dL	:	range of length group
$N_1, N_2,..$	:	total number of fish belonging to group 1, 2, .. (e.g. age-group)
$L_1, L_2,..$	:	mean length of group 1, 2, ...
$\sigma 1, \sigma 2,..$	:	width of group 1, 2, ...

The estimation problem, i.e. finding N_1, N_2, ..., $\bar{L}_1$, $\bar{L}_2$,..., and σ_1, σ_2, ..., in total 3 x k parameters, can be addressed in several ways.

Hasselblad (1966) and several subsequent authors discussed a least square solution, i.e.

$$\sum\left\{n(L) - N_1 \frac{dL}{\sqrt{2\pi}\,\sigma_1} \exp\left[-\frac{1}{2}\left(\frac{L-\bar{L}_1}{\sigma_1}\right)^2\right]\right\}^2 = \min$$

The minimum is found with respect to the parameters N_1, N_2, a.s.f. 3 x k parameters. This approach does not require any clean classes but is insensitive to small peaks. This may partly be overcome by dividing the squared difference by the theoretical (i.e., expected) number of fish for each term in the sum. Then this estimator is a chi-square estimator. Note that the number of length groups, K, is not part of the estimation problem; K must be known from elsewhere.