

Short Communication

Minor extension of the von Bertalanffy growth theory

M.R. Lipinski¹ and M.A. Roeleveld²

¹Marine Biology Research Institute, University of Cape Town, Rondebosch 7700 (South Africa)

²South African Museum, P.O. Box 61, Cape Town 8000 (South Africa)

(Accepted for publication 17 May 1990)

ABSTRACT

Lipinski, M.R. and Roeleveld, M.A., 1990. Minor extension of the von Bertalanffy growth theory. *Fish. Res.*, 9: 367-371.

The growth of "Growing Sealife"^(TM) plastic squid was tested against the principles of the von Bertalanffy growth theory. The von Bertalanffy growth curve fits the data well on visual inspection, although the Schnute curve actually provides a statistically superior fit. If the von Bertalanffy growth curve provides a reasonable fit to data, this is frequently interpreted as evidence for anabolic and catabolic changes. The results of this paper for plastic squid are intended to provide a warning that such an interpretation does not necessarily follow.

INTRODUCTION

The von Bertalanffy growth curve (von Bertalanffy, 1934, 1938) is probably the one most widely used in marine biology today. It is usually written in the form

$$l_t = l_\infty [1 - e^{-\kappa(t-t_0)}] \quad (1)$$

where l_t is the length of the animal at age t . The biological basis for this form is that growth represents the difference between anabolic and catabolic processes. Equation (1) then follows from the three assumptions that catabolism is proportional to mass, that anabolism is proportional to a surface area (because it is limited by the respiratory rate) and that growth is isometric (so that mass is proportional to l^3 and surface area to l^2). In a recent generalisation of von Bertalanffy's work, Pauly (1981) considers the evidence for and the consequences of non-isometric relationships between mass, surface area and length.

The combination of anabolic and catabolic processes, together with these three assumptions, implies that growth will follow the von Bertalanffy curve.

The main purpose of this paper is to warn that the reverse implication does not hold: the fact that eqn. (1) provides a reasonable fit to growth data is not necessarily evidence for constituent anabolic and catabolic processes.

MATERIALS AND METHODS

Twenty-two “Growing Sealife”^(TM) plastic squid were placed in tap water ($T = 13.7^\circ\text{C}$) and the mantle length of each individual was measured every 3–5 h over a 5-day period (Fig. 1). The von Bertalanffy and the Schnute (1981) growth curves were then fitted to the data by minimising the quantity

$$SS = \sum_{i,t} (l_{i,t} - \hat{l}_{i,t})^2 \quad (2)$$

where $l_{i,t}$ is the actual length of plastic squid i at time t , and $\hat{l}_{i,t}$ is the predicted length of squid i at time t given by the growth curve. The Schnute curve was fitted because it is a more general form and the von Bertalanffy curve has

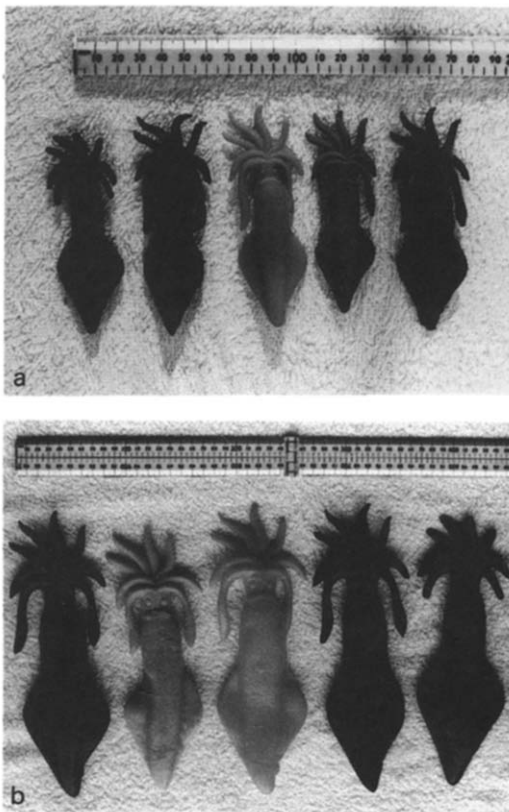


Fig. 1. Plastic squid before (a) and after (b) the growth experiment.

recently come under suspicion when applied to squid growth (Forsythe and Hanlon, 1989). Note that the Schnute growth curve may be written

$$l_t = [l_1^b + (l_2^b - l_1^b) \{1 - e^{-a(t-t_1)}\} / \{1 - e^{-a(t_2-t_1)}\}]^{1/b} \tag{3}$$

where $l_1 = l(t=t_1)$ and $l_2 = l(t=t_2)$ and a, b are the parameters of the Schnute's Generalised Growth Model (Schnute, 1981).

RESULTS AND DISCUSSION

Figure 2 shows the length data plotted against time, with the von Bertalanffy and Schnute curves superimposed. Although it appears, on inspection of Fig. 2, that the von Bertalanffy curve ($l_\infty = 176$ mm, $\kappa = 0.0324$ h⁻¹, $t_0 = -13.6$ h) fits the data satisfactorily, comparison with the Schnute curve fit ($a = 0.0435$, $b = 0.1146$, $l(t=0) = 64.8$ mm and $l(t=120) = 172$ mm) using the likelihood ratio test (Draper and Smith, 1966) indicates that the latter curve provides a statistically superior fit ($F = 12.66$; $df = 1,536$; $P < 0.01$). (Note that the von Bertalanffy curve is a special case of the Schnute form with $b = 1$.)

The fitting procedure used (which is that frequently applied when fitting age-length data to growth curves) does not, however, take into account the fact that the 540 data points available were provided by only 22 individuals, so that they are likely to be correlated. In other words, if a particular squid is

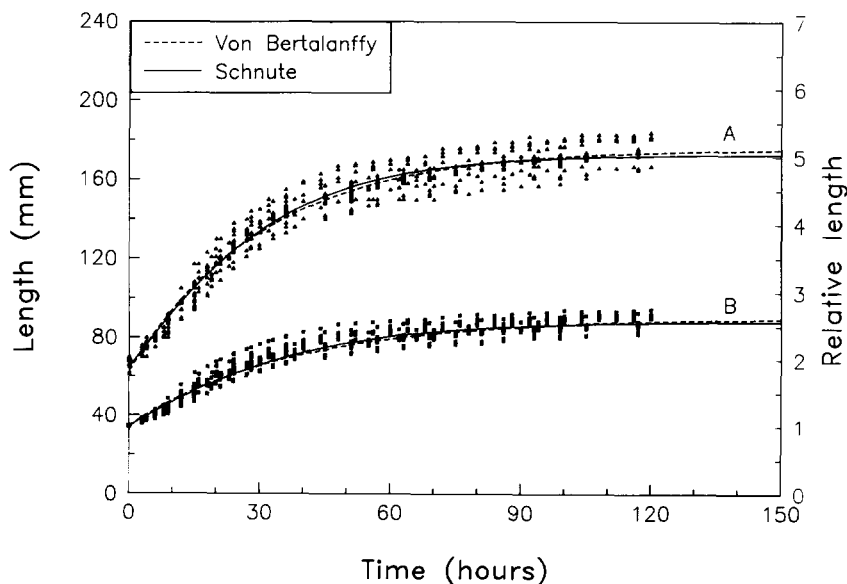


Fig. 2. Length data, shown by the triangles, plotted against time and fitted by the von Bertalanffy and Schnute growth curves (A). The relative length data (normalised to $l(t=0) = 1$) are shown by the squares, together with fits by the von Bertalanffy and Schnute growth curves taking autocorrelation into account (B).

below the average length for squid of the same age, it will very likely still be below average 3 or even 5 h later. This correlation effect invalidates the basis for the fitting procedure above in so far as any statistical inferences are to be drawn from the results, because these rest on the assumption that deviations from the predicted lengths are independent of each other. In order to overcome this problem, a revised fitting procedure was used.

(1) The data were recast in the form of a set of triplets

$$l_{i,t}; l_{i,t'}; \Delta t$$

where $l_{i,t}$ is the length of squid i at time t , $l_{i,t'}$ is the length when next measured at time $t' = t + \Delta t$ and Δt is the time difference (in hours) between the two readings.

(2) The revised data were normalised by dividing the length measurements for each squid by the length of the squid at the start of the experiment. This reduces the number of parameters to be fitted by one and is perhaps an acceptable simplification because the growth of the individuals is caused by absorption and bonding of water molecules, so that the ratio of final to initial length for each squid would be expected to be the same.

(3) The $l(t=0)$ parameter for the Schnute growth curve was fixed at 1.0; similarly the fit of the von Bertalanffy curve was constrained to pass through $l(t=0) = 1$. The curve parameters were then determined by minimising the quantity

$$SS' = \sum_{i,t'} (l_{i,t'} - \hat{l}_{i,t'})^2 \quad (4)$$

where $\hat{l}_{i,t'}$ is computed by using the growth parameters to calculate the time corresponding to $l_{i,t}$ and then evaluating the length Δt hours after this time from the growth equation.

The revised fits to the data, also shown in Fig. 2, are for von Bertalanffy: ($l_{\infty} = 2.640$, $\kappa = 0.0269 \text{ h}^{-1}$, $t_0 = -17.7 \text{ h}$) and for Schnute: ($a = 0.0377$, $b = 0.1217$, $l(t=0) = 1$, $l(t=120) = 2.555$).

The likelihood ratio test indicates that the Schnute curve remains a statistically superior fit ($F = 37.32$; $df = 1, 515$; $P < 0.001$). (Note that although these parameter estimates do not differ substantially from those obtained by minimising eqn. (2), the reason for this exercise is to be able to compare the fits of the two models on a sounder basis, so that our conclusion of evidence for model misspecification in the fit of the von Bertalanffy curve to the data is more defensible.)

CONCLUSIONS

(1) Assuming that a growth process is governed by the von Bertalanffy growth curve (even if it appears to fit the data well on visual inspection) is

not advisable unless appropriate fitting procedures are used, goodness of fit tests are performed (e.g. checking for systematic trends in the residuals) and comparisons are made with more generalised forms (e.g. the Schnute curve) to check for possible model misspecification. In the case of the plastic squid investigated here, there is actually statistically significant (even if relatively insubstantial) deviation from the von Bertalanffy curve.

(2) If a fit to growth data by the von Bertalanffy curve looks satisfactory, it does not therefore follow that this is evidence for anabolic and catabolic changes. The animal investigated might turn out to be a piece of plastic, now commonly found in our oceans (Ryan, 1988).

(3) Real squid are not unlike "Growing Sealife"^(TM): their growth may be described by the von Bertalanffy growth curve if desired (Pauly, 1985) and varies with temperature (Forsythe and Hanlon, 1989; Lipinski, personal observation). They are also a bit rubbery when cooked improperly.

ACKNOWLEDGEMENTS

Professor D.S. Butterworth and A.E. Punt (Department of Applied Mathematics, University of Cape Town) are acknowledged for their advice on the fitting procedures and alternative growth model used, and for carrying out the calculations. M.G. van der Merwe (South African Museum) is thanked for assistance with the illustrations. This work was supported by the Benguela Ecology Programme of the South African National Council for Oceanographic Research.

REFERENCES

- Draper, N.R. and Smith, H., 1966. *Applied Regression Analysis*. Wiley, New York, 709 pp.
- Forsythe, J.W. and Hanlon, R.T., 1989. Growth of the eastern Atlantic squid, *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda). *Aquacult. Fish. Manage.*, 20: 1–14.
- Pauly, D., 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Meeresforschung*, 28: 251–282.
- Pauly, D., 1985. Population dynamics of short-lived species, with emphasis on squids. *NAFO Sci. Coun. Stud.*, 9: 143–154.
- Ryan, P.G., 1988. The characteristics and distribution of plastic particles at the sea-surface off the southwestern Cape Province, South Africa. *Mar. Environ. Res.*, 25: 249–273.
- Schnute, J., 1981. A versatile growth model with statistically stable parameters. *Can. J. Fish. Aquat. Sci.*, 38: 1120–1140.
- Von Bertalanffy, L., 1934. Untersuchungen über die Gesetzlichkeit des Wachstums. I. Allgemeine Grundlagen der Theorie mathematische und physiologische Gesetzlichkeiten des Wachstums bei Wassertieren. *Roux Arch. Entwicklunsmech.*, 131: 613–652.
- Von Bertalanffy, L., 1938. A quantitative theory of organic growth (Inquiries on growth laws, II). *Hum. Biol.*, 10: 181–213.