

GROWTH AND GROWTH STUDIES

By J. Tang Christensen

Institute of Biological Sciences, Aarhus University, Ny Munkegade, 8000 Aarhus C, Denmark

ABSTRACT

Growth is a complex process. It is measured as a change in size, but its interpretation cannot be separated from other processes such as maturation and life history phenomena. Ultimately it must be viewed in the context of life history theory. Growth models, their interpretation, and the role of size and growth in the life histories of animals are briefly discussed.

INTRODUCTION

Size is an immediately perceptible and intuitively important feature of an organism. The rate at which size is attained and the influence of environmental fluctuations on this process plays an important role in ecology.

A diversity of factors influences growth rates. Recently, theoretical and empirical developments have focused on the importance of size and growth for other aspects of the life of an organism: mortality, fecundity, cost of maintenance and fitness. Such considerations do not constitute any method for studying growth, but they may form an important conceptual framework for designing studies and suggest what to look for. This challenge should be picked up by practical ecologists, through studies putting growth within the framework of the life history of organisms.

GROWTH MODELS

Growth trajectories tend to follow certain characteristic patterns. Often, but not always, growth is rapid at first and then levels off later in the life of an animal to approach an apparent asymptote. These patterns have puzzled researchers for many years, and they have, naturally, sought to reveal the logic behind them. A number of mathematical models behaving in similar ways have been proposed as formal descriptions of these patterns *viz.* the Bertalanffy equation, the Gompertz equation, the Richards equation and the logistic equation. Schnute (1981) has even proposed a comprehensive model including the

others as special cases. A certain similarity in pattern does not, however, constitute proof that the mathematical model is a valid description of the biological phenomenon in the sense that the parameters can be given well defined biological interpretations. Furthermore, parameters cannot be independently estimated. The models are empirical in the sense that parameter values are determined through a process of fitting.

Data may be in the form of size at age, growth increments or size-frequency data, each having advantages and drawbacks. Various methods of fitting models to data are available (Ford, 1933; Walford, 1946; Gulland, 1969; Schnute & Fournier, 1980; Kaufmann, 1981).

One of the more widely used of the empirical models is the von Bertalanffy growth equation. In its integrated form for growth in length it reads:

$$L(t) = L_{\infty} (1 - e^{-K(t-t_0)}), \quad 1)$$

The equivalent for growth in weight is:

$$W(t) = W_{\infty} (1 - e^{-K(t-t_0)})^3, \quad 2)$$

In both cases t_0 is the hypothetical age at which L and W , respectively, are equal to zero. L_{∞} and W_{∞} are asymptotic length and weight, respectively.

Models of natural phenomena tend to influence the way we think about these phenomena and we may easily forget the limitations of the models. In the case of the integrated form of the growth model it suggests that size is a function of age. However, it

is obtained by integration of a growth rate equation:

$$dW/dt = hW^n - kW^m \quad (3)$$

where hW^n represents synthesis of body substance (anabolism) and kW^m represents breakdown of substance (catabolism). These opposing processes are assumed to be proportional to certain powers of the body weight. One particular form of this equation with $n = 2/3$ and $m = 1$ is due to Pütter (1920) and the models 1) and 2) result from integration of this equation (Bertalanffy, 1934; Beverton & Holt, 1957). Pütter's equation is a physiological model assuming synthesis of body substance to be proportional to the absorbing surfaces of the body (hence, the $2/3$ power of weight). It also assumes that food is not limiting.

Looking at the differential growth rate equation it is obvious, that growth rate is determined by body weight, which also makes sense from metabolic considerations. Thus, size is only superficially a function of age, and only so if conditions of growth remain constant. This distinction may seem trivial, but the important point to be made is, that the physiological interpretation is only valid, if growth follows the same trajectory throughout the life of the animal, and food is not limiting. But animals live in fluctuating environments and their growth rates fluctuate accordingly. In addition to such formal problems other criticism has been advanced (Knight, 1968; Roff, 1980).

Given the statistical scatter frequently observed in ecological data, models of these types are sufficiently flexible to be made to fit almost any curve. At best, fitting an empirical model should be considered as a convenient means of summarizing the data. What such models do not reveal are the genetical and environmental mechanisms underlying the patterns. Physiological models of growth may take the form $\Delta G = \Delta F - \Delta M$, where ΔF is the amount of useful energy assimilated from the food during a unit of time, and ΔM is the energy required for maintenance. This model bears some resemblance to the Pütter equation forming the basis of the von Bertalanffy

equation, and may produce similar (though not mathematically identical) results under certain assumptions. Within this framework W_∞ may be interpreted as the weight at which an animal, at a certain resource level, is just able to balance assimilated energy against the amount used for activity and maintenance.

The problem with further development of this model is that maintenance requirements are not only related to size, but also depend in complex ways on amount of available food and growth rate. Assimilated energy is correlated to size as well.

Empirical relationships between metabolic rate, temperature and level of activity have been established for different animal groups (Jones, 1976). Such studies are useful as at least they confirm, that insight in the mechanisms of growth cannot be gained through analysis of patterns alone. It is necessary to look at instantaneous events, not just at averages of highly variable, interrelated processes. However, these studies do not explain why members of some species invariably grow to larger sizes than members of other species. There must be some sort of internal control of growth. Genetically determined variation in growth rate has been found even within species (Rawson and Hilbish, 1991).

Why do animals grow at all? Why waste time and energy on it? A logical answer to this question is, of course, that there is some advantage to being big. Thus, we may ask, what role does size play in the fitness of an animal?

GROWTH IN THE CONTEXT OF NATURAL SELECTION

The concept of fitness is central to the idea of evolution through natural selection. But fitness is difficult to measure, because it is not a property of an animal or a phenotype, but of that animal or phenotype in its environment! The fittest organism is the one that contributes the most to future generations. Clearly, reproduction is important, but not the only contributor to fitness. Size, and hence growth, has a role to play too. Consider the basic biological processes of an organism: maintenance, growth and reproduction. These processes compete for the lim-

ited time and resources available to the organism. A life-history strategy may be seen as the allocation of resources between these processes in an attempt to maximize fitness (Gadgil and Bossert, 1970; Stearns, 1976).

Size is positively correlated to fitness attributes such as fecundity, reproductive effort, mating success, competitive ability, survival, etc. But growing big takes time, and time may be in short supply because the organism should reproduce before being lost to mortality. The age at which sexual function is attained (age at maturity) has a direct effect on fitness. In expanding populations earlier-born progeny have a greater impact on population growth than later born progeny, and in stable populations age at maturity is thought to evolve so as to maximize lifetime reproductive success. Thus, opposing forces are at play.

Somatic growth may superficially be seen as a continuous process, but looking at it in greater detail it is evident, that it is not. Many animals grow only during resting periods. Growth is determined by instantaneous events of resource allocation. During periods of frequent allocation to growth, the growth trajectory will rise more steeply than during periods of infrequent allocation. The size of an animal at a particular age is a point along the growth trajectory.

Maturity is usually a reasonably well defined stage in the development of an organism. But maturity is just a point along the differentiation trajectory of the organism. Thus, size and degree of development at any particular time, are just points along the trajectories of growth and differentiation, respectively (Bernardo, 1993). These trajectories are correlated through age, and it has been experimentally confirmed, that genetic correlations exist. The accumulation over time of instantaneous events of allocation of limited resources to either growth, differentiation, etc., results in a specific size and age at maturity - an important feature of an animals life-history strategy.

Controversy still exists as to what limits animals and plants. Energy is often chosen as the common currency. Energetic limitation of organisms implies the importance of optimal energy allocation for size

and age at maturity. Each energy unit allocated to growth could, in principle, be allocated to reproduction, and *vice versa* (Kozlowski, 1992). Investing in growth means investing in better survival and possibly greater future reproduction

The problem of optimal energy allocation is very complex and mathematical treatment of specific problems requires many assumptions. Another problem with this theory is to decide on a measure of fitness, *i.e.* what to maximize. In life history studies the measure of fitness most often used, in the absence of density effects, is r , the intrinsic rate of increase. In allocation theory expected lifetime allocation of energy to reproduction is maximized. This is equivalent to lifetime offspring production, if the amount of energy invested per offspring is constant. Again, lifetime offspring production is equivalent to r only under the assumption of a constant population size. Thus, if we want to avoid unrealistic assumptions, combining these theoretical frameworks is difficult without introducing more complexity than we may be able to handle. But theoretical studies with limiting assumptions may point to interesting fields of investigation for the field ecologist (Roff, 1981; Stearns and Koella, 1986).

In conclusion: Growth trajectories are the result of instantaneous events accumulated over time. In view of the complexity of the interrelated processes involved in producing patterns of growth, a universal, mechanistic model is not the thing to look for. Growth is a far too complicated process to be described in a biologically meaningful way by a mechanistic model with a few parameters. Instead, theoretical considerations may point to interesting fields of research where insight can be gained.

Because growth cannot be separated from other aspects of an organisms life, growth studies should be designed within the conceptual framework of life history theory and optimal resource allocation theory. Size and age at maturity are important, measurable parameters which can relate empirical studies of populations to this theory. As suggested by Bernardo (1993), descriptive and experimental studies of populations exhibiting interdemical variation in growth rate, size, and age at maturity are likely to provide fruitful insights. Populations of the same

species from different localities may be compared, and groups from the same population may be exposed to different environments, to elucidate genetic variation and phenotypic plasticity. This way, basic

knowledge of determinants of growth can be gained. The Tropical Marine Mollusc Programme, with its wide geographic coverage, is uniquely suited to take up this challenge.

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