

# Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction

N. P. Lester<sup>1,2\*</sup>, B. J. Shuter<sup>1,2</sup> and P. A. Abrams<sup>1</sup>

<sup>1</sup>Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5, Canada

<sup>2</sup>Aquatic Research and Development, Ontario Ministry of Natural Resources, Peterborough, Ontario K9J 8M5, Canada

We develop a model for somatic growth in fishes that explicitly allows for the energy demand imposed by reproduction. We show that the von Bertalanffy (VB) equation provides a good description of somatic growth after maturity, but not before. We show that the parameters of the VB equation are simple functions of age at maturity and reproductive investment. We use this model to show how the energy demands for both growth and reproduction trade off to determine optimal life-history traits. Assuming that both age at maturity and reproductive investment adapt to variations in adult mortality to maximize lifetime offspring production, our model predicts that: (i) the optimal age of maturity is inversely related to adult mortality rate; (ii) the optimal reproductive effort is approximately equal to adult mortality rate. These predictions are consistent with observed variations in the life-history traits of a large sample of iteroparous freshwater fishes.

**Keywords:** fish; somatic growth; reproductive investment; Bertalanffy growth model; optimal life histories

## 1. INTRODUCTION

The von Bertalanffy (VB) growth equation is widely used to describe the lifetime pattern of somatic growth in fishes (e.g. Ricker 1975) and other organisms that exhibit indeterminate growth. Although there is strong empirical support for this model (e.g. Chen *et al.* 1992), it has been argued on theoretical grounds that a single somatic growth equation cannot describe lifetime growth patterns because it cannot cleanly account for the change in energy allocation that occurs with maturity (Day & Taylor 1997; Czarnoleski & Kozłowski 1998). Day & Taylor (1997) suggested that the somatic growth trajectory should be specified by two separate equations: a pre-maturity equation in which all surplus energy is devoted to somatic growth, and a post-maturity equation in which some or all surplus energy is devoted to reproduction. Charnov (1993) and Charnov *et al.* (2001) provided explicit developments of this idea and showed that the shape of the lifetime growth curve is strongly influenced by both age at maturity and degree of reproductive investment. We build on this work by developing a simple lifetime growth model, founded on empirically justified approximations of the allometric functions governing net biomass production in fishes. For this model, the VB equation provides an exact description of post-maturation somatic growth and the parameters of the VB equation contain useful information on both age at maturity ( $T$ ) and degree of reproductive investment ( $g$ ). We then use the model to evaluate how trade-offs between somatic growth and reproduction determine optimal life-history traits.

We begin with the *potential* lifetime growth pattern, assuming no reproduction. Because consumption is limited by foraging time (e.g. Holling 1959) and the processing capacity of the digestive tract (e.g. Reiss 1989),

both the quantity and quality of available food (i.e. the prey field) will affect potential growth. In addition, the abundance and relative effectiveness of predators (i.e. the predator field) will affect growth because increased predation risk often suppresses foraging activity (Turner & Mittelbach 1990; Fraser & Gilliam 1992; Eklöv & Persson 1995; Lima 1998). We include simple representations of these ecological effects in our model of growth in early life. We go on to show how these somatic growth patterns change when a fish becomes sexually mature and energy is diverted from somatic growth to reproduction. The realized lifetime pattern for somatic growth is shaped by two decisions: when to invest in reproduction ( $T$ ) and how much energy to invest ( $g$ , the joint cost of gamete production and the behavioural activities associated with reproduction). Following Charnov *et al.* (2001), we assume that both  $T$  and  $g$  adjust to differences in adult mortality to maximize the lifetime production of offspring by a typical female. We then evaluate how the optimal values for  $T$  and  $g$  vary in response to variations in adult mortality and compare these predicted values with observed  $T$  and  $g$  values for a large sample of freshwater fish species.

## 2. POTENTIAL SOMATIC GROWTH

Bioenergetics models developed for fishes indicate that potential somatic growth rate (i.e. net production) scales allometrically with fish weight:

$$dW/dt = c_1 W_t^{m_1} - c_2 W_t^{m_2}, \quad (2.1)$$

where  $W_t$  is somatic weight,  $c_1 W_t^{m_1}$  is the rate of energy acquisition and  $c_2 W_t^{m_2}$  reflects energy losses owing to respiration (e.g. standard metabolism and activity). Out of the 26 fish species modelled by Hanson *et al.* (1997), ca. 75% have  $m_1$  and  $m_2$  values that lie in the range 0.66–0.80, with mean values of 0.69 and 0.78, respectively. Reiss (1989) cites similar values (0.67 and 0.75,

\* Author for correspondence (nigel.lester@mnr.gov.on.ca).

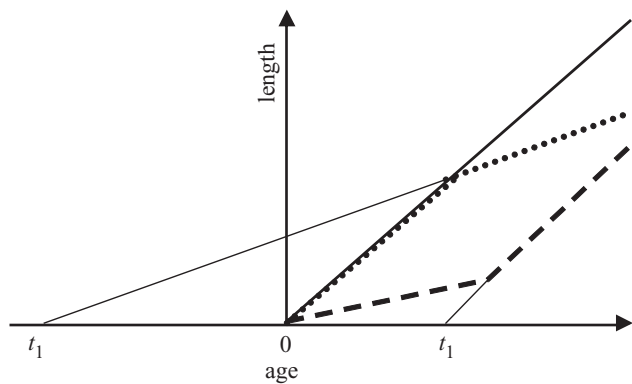


Figure 1. Influence of prey and predator fields on potential somatic growth of fishes. Solid line through the origin represents growth when the prey field is extensive and predators are absent; dotted line represents growth when the prey field is truncated and predators are absent; dashed line represents growth when the prey field is extensive but early growth is inhibited owing to avoidance of predators.

respectively), based on his survey of the literature. Clarke & Johnston (1999) provide an extensive review of the newer fish literature and show that values for  $m_2$  range from 0.5 to 1.0, with a modal value of 0.7. Since much of the literature suggests that  $m_1$  and  $m_2$  have similar values that both lie close to 2/3, we assumed that the following equation holds:

$$dW/dt = (c_1 - c_2) W_t^{2/3}. \tag{2.2}$$

This assumption permits us to develop a simple model structure for somatic growth while introducing only a relatively small error into our representation. The error is negligible (less than ±10%; Appendix A) provided  $m_1$  and  $m_2$  have similar values within the range 0.67–0.70. It grows to ±30% as the value for the joint exponent increases to 0.75. Given that weight increases with the cube of length ( $W = aL^3$ ), then the potential growth rate for length (e.g. cm yr<sup>-1</sup>) is

$$dL/dt = h_0, \tag{2.3}$$

where  $h_0 = (c_1 - c_2)/3a^{1/3}$  and thus length is a simple linear function of time ( $L_t = h_0t$ ; solid line in figure 1), assuming that size at ‘birth’ is effectively zero.

This model assumes that the balance ( $c_1 - c_2$ ) between the energy gained from foraging and the energy used in foraging and maintenance does not change as fishes grow. Many fishes, particularly top predators, exhibit ontogenetic diet shifts, moving successively from smaller to larger prey items as they grow. If such a species lives in a community where a broad range of prey sizes is available, the transition to larger prey occurs smoothly as the individual grows (Paloheimo & Dickie 1966; Kerr 1971; Kerr & Ryder 1977; Piazza *et al.* 2002), equation (2.3) is likely to hold throughout life, and potential length growth rate remains constant. If the prey field is truncated such that the availability of prey of suitable size does not keep pace with increases in predator size, then the slope of the potential growth curve ( $c_1 - c_2$ ) will decline (dotted line in figure 1) owing to the increases in foraging costs associated with capturing relatively smaller prey (Piazza *et al.* 2002). This decline in growth can be approximated using a new growth curve:

$$L_t = h_1 (t - t_1), \tag{2.4}$$

where  $t_1$ , the intercept on the time axis for the new curve, decreases from zero in parallel with both the difference ( $h_0 - h_1$ ) and the age at which the transition from  $h_0$  to  $h_1$  occurs. Those species that grow to large adult sizes are more likely to outgrow their prey fields and hence exhibit growth curves with negative  $t_1$  values.

The nature of the predator field may also influence potential growth through its impact on foraging activity. For most fishes, predation risk is high early in life and declines rapidly as the individual grows. Thus, the role of predator-avoidance behaviour in depressing foraging activity, and thus growth (Lima 1998), will be greatest early in life and will decline as the fish grows out of its predator field (dashed line in figure 1): growth early in life will equal  $h_0t$  and later it will equal  $h_1(t - t_1)$ , with  $t_1$  increasing from zero in parallel with both the difference ( $h_1 - h_0$ ) and the age at which the transition from  $h_0$  to  $h_1$  occurs. Those species that grow to small adult sizes are more likely to exhibit growth curves with positive  $t_1$  values because their growth curves will be free of the obscuring influence of prey field effects.

### 3. SOMATIC GROWTH WITH REPRODUCTION

The potential growth model developed above assumes that all surplus energy is allocated to somatic growth. It does not account for the change in somatic growth that occurs when fishes become sexually mature and some energy is allocated to reproduction. For many fish species, the annual physical (as distinct from behavioural) investment in reproduction ( $g = \text{gonad weight/somatic weight}$ ) for a typical female is fairly constant throughout her reproductive lifetime (table 1 in Roff 1983). A constant proportional allocation to reproduction produces post-maturation growth that is described by a VB growth function (Appendix B):

$$L_t = L_\infty (1 - e^{-k(t-t_0)}), \tag{3.1}$$

where

$$L_\infty = 3h_1/g, \tag{3.2}$$

$$k = \ln(1 + g/3), \tag{3.3}$$

$$t_0 = T + \ln(1 - g(T - t_1)/3)/\ln(1 + g/3). \tag{3.4}$$

The resultant lifetime growth curve (figure 2) is linear until age  $T$  and then becomes asymptotic, following equation (3.1). The feasible range for  $g$  is  $(0, 3/(T - t_1)]$ : growth is indeterminate if  $g < 3/(T - t_1)$  and determinate if  $g = 3/(T - t_1)$ . If growth is determinate, then  $L_\infty$  equals length at maturation ( $L_T$ ). Thus, the expected lifetime growth pattern depends on both  $T$  and  $g$ .

### 4. OPTIMAL REPRODUCTIVE STRATEGIES

Given a stable population regulated by density-dependent processes at very young ages, with a mortality rate ( $M$ ) throughout the later juvenile and adult stages, we expect that selection will act to maximize  $R_0$ , the lifetime output of female offspring by a typical female (Charlesworth 1994):

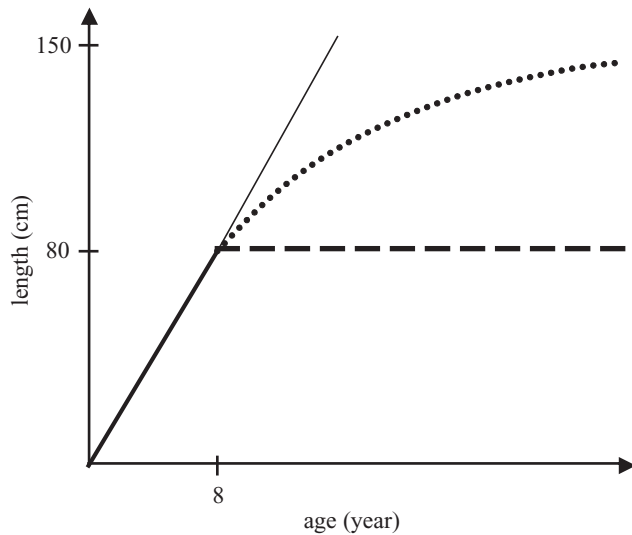


Figure 2. Influence of reproduction on somatic growth assuming  $h_1 = h_0 = 10 \text{ cm yr}^{-1}$ . Solid line represents growth if all surplus energy is allocated to soma; dotted line represents growth if allocation is to reproduction as follows:  $T = 8$  years,  $g = 0.2 \text{ yr}^{-1}$ ; dashed line represents growth with allocation to reproduction as follows:  $T = 8$  years,  $g = 3/T = 0.375 \text{ yr}^{-1}$ .

$$R_0 = \sum_{t=T+1}^{\infty} s e^{-Mt} \text{fec}_t, \quad (4.1)$$

where  $T + 1$  is the initial age of spawning (1 year after allocation to reproduction begins),  $M$  is the instantaneous mortality rate ( $\text{yr}^{-1}$ ),  $s$  is an early survival parameter (i.e. survival from egg to age 1 is  $se^{-M}$ ) and  $\text{fec}_t$  is number of female eggs produced by a female spawning at age  $t$ . Our growth model implies

$$\text{fec}_t = g W_t / 2w_e, \quad (4.2)$$

where  $w_e$  is mean egg weight and the numerator is divided by 2 to give the number of female eggs (1 : 1 sex ratio assumed). Given  $W = aL^3$ , then

$$\text{fec}_t = g a L_t^3 / 2w_e \quad (4.3)$$

and given equations (3.1)–(3.4), equation (4.1) expands to

$$R_0 = \frac{27sah_1^3}{2w_e} \sum_{t=T+1}^{\infty} \frac{e^{-Mt}}{g^2} \times \left( 1 - \left( 1 - \frac{g}{3} (T - t_1) \right) \left( \frac{3}{3+g} \right)^{t-T} \right)^3, \quad (4.4a)$$

which yields the following closed form:

$$R_0 = \frac{27sah_1^3}{2w_e} \left\{ \frac{e^{-MT}}{g^2} \left[ \frac{1}{e^M - 1} + \frac{3(g(T - t_1) - 3)}{e^M(3 + g) - 3} \right] + \frac{3(g(T - t_1) - 3)^2}{e^M(3 + g)^2 - 9} + \frac{(g(T - t_1) - 3)^3}{e^M(3 + g)^3 - 27} \right\}. \quad (4.4b)$$

Parameters on the left side of the braces,  $\{\}$ , in equation (4.4b) act as multipliers, affecting the absolute value of  $R_0$ , but not the values of  $T$  and  $g$  which maximize it. In a population maintained at equilibrium by density-dependent effects,  $R_0$  must equal 1. In populations where

equilibrium is maintained by density-dependent effects operating on the multipliers to the left of the braces, then selection will produce an evolutionary stable strategy characterized by values of  $g$  and  $T$  that maximize the quantity inside the braces (Mylius & Dieckmann 1995).

If growth is determinate, then  $g = 3/(T - t_1)$ , and the summation term is maximized when  $T - t_1$  equals  $2/M$  (Appendix C); therefore  $g = 1.5M$ . For  $M$  in the range of 0.05–1.0, we used numerical methods to show that, for indeterminate growth ( $g < 3/(T - t_1)$ ), the summation term is a convex function of  $g$  and  $T$  with a single maximum that exceeds the maximum for determinate growth and is closely approximated by the following empirical functions of  $M$ ,

$$(T - t_1) \approx 1.95/(e^M - 1), \quad (4.5)$$

$$g \approx 1.18 (1 - e^{-M}). \quad (4.6)$$

For  $M$  in the range of 0.05 to 1.0, the difference between the exact value of  $T$  and the value given by equation (4.5) is less than 0.3 years and the difference between the exact value of  $g$  and the value given by equation (4.5) is less than  $0.02 \text{ yr}^{-1}$ . The optimal rate of reproductive investment ( $g$ ) depends solely on  $M$ , whereas the optimal age of maturity depends on both  $M$  and  $t_1$ . As expected, the optimal solution for indeterminate growth specifies somewhat earlier maturity and lower investment than the optimal solution for determinate growth.

## 5. EMPIRICAL SUPPORT FOR THE MODEL

The VB curve has been used extensively to describe the growth of exploited fish populations. Typically these descriptions are based on data from harvested fishes that are dominated by mature individuals. Ricker (1975, p. 225) noted that the VB equation typically provided a good description of growth later in life and that ‘In fitting the curve, the main thing is to avoid including younger ages that do not conform to it’. Semelparous species provide clear examples of pre-maturation growth patterns. Ocean growth of immature Pacific salmon is summarized for four species in Groot & Margolis (1991): the data show that growth in length is essentially linear over time periods of up to 4 years and length increases from 2- to 10-fold. This finding matches the behaviour expected from our model. Both Ursin (1967) and Essington *et al.* (2001) fitted equation (2.1) to population-specific somatic growth data from several species. In most cases, the data were dominated by older mature fishes and thus the estimates for  $m_1$  and  $m_2$  that they derived actually represent the exponents for net production and reproductive allocation in our model, rather than the exponents for consumption ( $m_1$ ) and maintenance-activity costs ( $m_2$ ) as defined for equation (2.1). Their estimates for  $m_1$  (0.59,  $n = 81$  species (Ursin) and 0.69,  $n = 14$  (Essington), respectively) and  $m_2$  (0.83,  $n = 81$  (Ursin) and 1.0,  $n = 4$  (Essington), respectively) are consistent with the values used in our model to represent net production and reproductive allocation.

We used the Randall & Minns (2000) compendium of life-history data (age of maturity  $T$ , length at maturity  $L_T$ , maximum length assumed equal to  $L_\infty$ , adult mortality  $M$  estimated from maximum lifespan using the method of

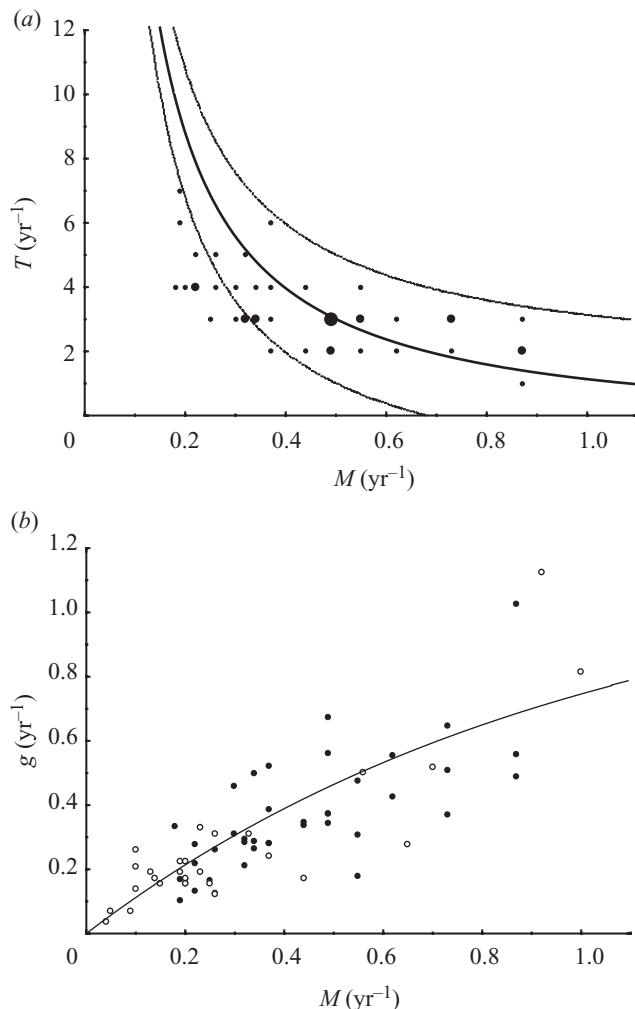


Figure 3. Predicted and observed relationships between mortality rate ( $M$ ), age of maturation ( $T$ ) and reproductive effort ( $g$ ) for species with  $M < 1.0$ . In (a), the solid line is the predicted  $T$  versus  $M$  relationship from equation (4.5), with  $t_1$  set to zero; the dotted lines are predictions for  $t_1 = -2$  and  $t_1 = +2$ ; the size of each dot is related to the number of cases (one, two or three species). In (b), the solid line is the predicted  $g$  versus  $M$  relationship from equation (4.6); the closed circles are indirect estimates of  $g$  derived from somatic growth parameters presented in Randall & Minns (2000); the open circles are direct estimates of  $g$  derived by multiplying the gonad–soma wet weight ratios of Gunderson (1997) by 1.73.

Hoening (1983)) for Canadian freshwater fish species to assess whether the optimal life-history strategies summarized in equations (4.5) and (4.6) are realized in nature. There is a strong association between  $T$  and  $M$  (figure 3a) that is quantitatively similar to equation (4.5): given a range for  $t_1$  of  $(-2, 2)$ , predicted values for  $T$  encompass most of the observed values. We estimated  $t_1$  for each species by substituting empirical estimates of  $T$  and  $M$  in equation (4.5) and solving for  $t_1$ . These  $t_1$  values exhibited a strong negative association with  $L_\infty$  ( $R^2 = 0.35$ ,  $n = 42$ ,  $p < 0.0001$ ):

$$t_1 = 0.55 - 0.033 L_\infty. \quad (5.1)$$

This result is consistent with our expectation that species with smaller adult body sizes are more likely to exhibit the positive  $t_1$  values characteristic of size-dependent predator

avoidance, whereas species with larger adult body sizes are more likely to exhibit the negative  $t_1$  values associated with truncated prey fields. To compare the Randall & Minns (2000) dataset with equation (4.6), we needed to derive estimates of  $g$  from their data. From equations (3.2) and (3.3), it is evident that the shape of the post-maturity, VB phase of the growth curve is set by the value of  $g$  and thus an indirect estimate of  $g$  can be obtained from the growth curve parameters themselves. Rearrangement of equations (2.4) and (3.2) shows that  $g$  equals  $3(L_T/(T - t_1))/L_\infty$  and since estimates of  $L_T$ ,  $L_\infty$ ,  $T$  and  $t_1$  were available for all the species in the Randall and Minns dataset, we could use this formula to obtain indirect estimates of  $g$  for each of them. These indirect estimates of  $g$  were positively associated with  $M$  (figure 3b) in a manner consistent with equation (4.6). Figure 3b also plots direct estimates of  $g$  against  $M$ , for 28 species of marine and freshwater fishes, derived from data presented in Gunderson (1997). Gunderson reported values for the wet weight ratio of gonad mass to body mass. This figure underestimates the true value of  $g$  because it does not account for the fact that the energy content per unit *wet weight* of gonad is typically higher than that for somatic tissue. We found several studies in the literature with the data necessary to estimate the energy ratio of gonad to soma on a wet weight basis: Gunderson & Dygert (1988) six marine species, median value = 1.6; Srivastava & Brown (1991) *Salmo salar* 2.0; Lahti & Muje (1991) *Coregonus albula* 1.76; Henderson & Nepszy (1994) *Sander vitreus* 1.4; Henderson *et al.* (2000) *Perca flavescens* 1.24. The value for the energy multiplier that gives the best match between Gunderson's data and equation (4.6) is 1.73 and this is the value we used in plotting the data in figure 3b. Both the indirect and direct estimates of  $g$  in figure 3b are consistent with equation (4.6) and thus both datasets provide independent support for the model. It is perhaps not too surprising that the value of the multiplier (1.73) needed to bring Gunderson's gonad weight ratios into line with equation (4.6) is at the high end of the measured energetic conversion factors for gonad:  $g$  also includes energy associated with the behavioural aspects of reproduction and thus, for some species, the 'true' value of  $g$  would be expected to exceed the value calculated strictly from the allocation of energy to gonad.

Other fish life-history datasets are consistent with equations (4.5) and (4.6). For example, Charnov (1993) summarized maturation data from many fish species and concluded that age of maturity ranged from  $1.75/M$  to  $2.2/M$ . This finding is consistent with equation (4.5) when  $t_1$  values are not extreme.

## 6. DISCUSSION

Empirically, the VB equation provides effective descriptions of somatic growth in fish (Chen *et al.* 1992), yet theory suggests that a single equation should be incapable of accounting for both pre- and post-maturation growth (e.g. Day & Taylor 1997). Our model implies that the VB equation is an appropriate model for describing adult somatic growth—the characteristic asymptotic shape arising primarily from the allocation of energy to reproduction—however, it is not appropriate for describing pre-maturation growth. Bioenergetic parameters imply

that somatic growth for this life stage will be roughly linear. Therefore, the lifetime growth pattern is a mixture of two models (figure 2), with the dominant model determined by the relative duration of pre- and post-maturation life stages. The widespread and successful use of the VB curve to describe fish growth suggests that the post-maturation phase dominates the length-at-age data that are usually available. This dominance is expected because the post-maturation phase is typically two to three times longer than the pre-maturation phase in iteroparous fish species. In addition, this dominance can be exacerbated by sampling protocols (e.g. commercial fishery procedures) directed at capturing larger individuals and avoiding the immature fishes needed to characterize pre-maturation growth. Data from semelparous fish species provide a better opportunity to observe pre-maturation growth patterns, and the Pacific salmon data suggest that this pattern is approximately linear rather than asymptotic.

Our model offers a biological interpretation of the VB growth parameters ( $L_\infty$ ,  $k$ ,  $t_0$ ). These quantities are usually regarded as mere phenomenological descriptors. However, our model shows that they reflect the reproductive biology of the animal:  $k$  is set by the magnitude of reproductive investment ( $k \approx g/3$ );  $L_\infty$  is set by the ratio of net production to reproductive investment ( $L_\infty = 3h_1/g$ );  $t_0$  is a simple function of  $T$  and  $g$ . Thus, the somatic growth curve for adult females can be a useful source of information on female reproductive behaviour. However, this requires that the curve be derived exclusively from adult data.

Kozlowski (1996) showed that, in a seasonal growth environment, the optimal reproductive strategy for animals that are constrained to direct assimilated energy either to somatic growth or reproduction is an indeterminate growth strategy: in the growing seasons that follow first maturity, a period of somatic growth should precede a period of reproductive allocation. Our model confirms this conclusion: if we assume simultaneous allocation of energy to somatic growth and reproduction, then the optimal reproductive strategy is a determinate growth strategy. If we impose constraints that: (i) reproduction can occur only once per year; (ii) the reproductive event must be preceded by a period of energy allocation to the gonad; (iii) energy can be allocated to soma or to gonad, but not to both simultaneously, then the optimal strategy is an indeterminate growth strategy. Because the typical behaviour of fish species living in seasonal growth environments is consistent with the existence of these constraints (e.g. Wootton 1999, p. 161), their existence seems to provide a sufficient explanation for the frequent observation of indeterminate growth among this group of animals.

Our model also illustrates how the ecological environment of an animal can impact its reproductive decisions (equation (4.5)). If the lifetime prey field for a fish is truncated and provides only small prey, then the optimal age for maturation will be reduced. If the prey field is ideal, but early growth is inhibited owing to predator avoidance (Abrams & Rowe 1996), then the optimal age of maturation will be increased. Of course, a scarcity of large prey need not always imply early maturity and small adult size: species that inhabit environments that provide high concentrations of small prey and low levels of adult mortality will have high  $T$  and  $L_\infty$  values, and the  $L_\infty$  value

will be enhanced if the species has developed morphological specializations to enhance its feeding efficiency on smaller prey.

In accounting for the trade-off between somatic growth and reproductive investment, equations (4.4) provide a general structure for evaluating how reproductive traits should adapt to a variation in  $M$ . In our development of the model, we focused on female behaviour, under the assumption that the cost of gonadal development dominates other costs associated with reproduction (e.g. changes in body coloration and morphology, courtship and nest defence). This assumption rarely holds for males because the energy demand for sperm production is much less than that for eggs. To study optimal reproductive strategies in males one would need to develop a male 'fecundity' function that describes how energy invested in such activities as courtship and brood defence contributes to male reproductive success. In many fish species, males mature earlier, attain a smaller asymptotic size, and have higher adult mortality rates than females. These differences imply that the trade-off structures that determine male reproductive strategies differ in a consistent and systematic fashion from those that shape female behaviour.

This paper is similar to earlier treatments of optimal life histories with indeterminate growth, notably Roff (1984), Ylikarjula *et al.* (1999) and Charnov *et al.* (2001). Since our analysis most closely parallels that of Charnov *et al.* (2001), we will briefly discuss the differences between their work and ours. Charnov *et al.* (2001) assume that an increase in allocation to reproduction requires a proportional increase in metabolic maintenance and activity costs. This assumption is required to obtain an evolutionary optimum other than determinate growth in their model; however, no empirical evidence is presented to support it. In our model, indeterminate growth arises naturally from the seasonal nature of reproduction and the requirement that investment into reproduction must occur prior to the actual event. Another major difference is that Charnov *et al.* (2001) assume that the exponents in equation (2.1) are unequal, with  $m_1 = 0.75$  and  $m_2 = 1$ . This means that juvenile length growth is asymptotic rather than linear and that adult growth must be represented by a more complex asymptotic growth equation with parameters that do not bear the same simple relation to somatic growth and reproduction as the parameters in our model. The predictions of the two models differ in a variety of other ways. We will discuss two of these differences in detail: (i) the relation between mortality and the product of lifespan and optimal age at first reproduction differs under the two models; Charnov (1993; see also Charnov *et al.* 2001) argues that the age at maturity divided by average adult lifespan should be a constant (approximately 2)—this quantity is closer to 2, and varies less with adult mortality, under our model (1.85–1.92 for adult lifespans between 1 and 20 years) than under the model in Charnov *et al.* (2001; see their figure 3); (ii) the model in Charnov *et al.* (2001) predicts that the ratio  $g/M$  should range from 0.5 to 0.65 whereas our model predicts a value closer to 1.0; a value close to 1.0 is more consistent with the data presented in figure 3*b*.

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**APPENDIX A: SENSITIVITY OF LENGTH GROWTH TO VARIATION IN THE WEIGHT EXPONENT FOR NET PRODUCTION**

For many freshwater fish species, the increase in length from age 1 to maturity is less than or equal to a factor of 10 (Carlander 1969, 1977, 1997). Given a 10-fold increase in length, if  $m_1 \approx m_2 = 0.70$ , then  $h_0$  in equation (2.3) varies by *ca.* less than  $\pm 10\%$  over the pre-maturity length range; if  $m_1 \approx m_2 = 0.75$ , then  $h_0$  varies by *ca.*  $\pm 30\%$ .

**APPENDIX B: PROOF THAT POST-MATURATION GROWTH IS A VON BERTALANFFY PROCESS**

Assume:

- (i) a cubic somatic weight ( $W$ )–length ( $L$ ) relationship  $W_t = aL_t^3$ ;
- (ii) an annual growing season of  $D$  days: for the first  $d$  days, net production is allocated to somatic growth; for the remaining  $(D-d)$  days, it is allocated to reproduction Kozlowski (1996);
- (iii) a daily net production during the reproductive life-span of  $dW/dt = cW^{2/3}$ ;
- (iv) that gonad weight at the end of year  $t$  is proportional to somatic weight:  $G_{t+1} = gW_{t+1}$ .

Thus, somatic weight ( $W_{t+1}$ ) and gonad weight ( $G_{t+1}$ ) at the end of each year when spawning occurs are

$$W_{t+1} = (W_t^{1/3} + cd/3)^3, \tag{B 1}$$

$$G_{t+1} = c W_{t+1}^{2/3} (D - d). \tag{B 2}$$

Given isometric growth (assumption (i)) and letting  $p_t = d_t/D$  be the proportion of the growing season when surplus energy is devoted to somatic growth,

$$L_{t+1} = L_t + cDp_t/3a^{1/3}, \tag{B 3}$$

$$G_{t+1} = L_{t+1}^2 a^{2/3} cD (1 - p_t). \tag{B 4}$$

Letting  $h_1 = cD/3a^{1/3}$ , these equations become

$$L_{t+1} = L_t + h_1 p_t, \tag{B 5}$$

$$G_{t+1} = L_{t+1}^2 3ah_1 (1 - p_t). \tag{B 6}$$

Given assumption (iv), equation (B 6) becomes

$$gW_{t+1} = L_{t+1}^2 3ah_1 (1 - p_t) \tag{B 7}$$

and therefore

$$gaL_{t+1}^3 = L_{t+1}^2 3ah_1 (1 - p_t),$$

implying

$$p_t = 1 - (g/3h_1) L_{t+1}. \tag{B 8}$$

Substituting for  $p_t$  in equation (B 5) implies

$$L_{t+1} = (3/(3 + g)) L_t + 3h_1/(3 + g). \tag{B 9}$$

For VB growth,

$$L_{t+1} = e^{-k} L_t + L_\infty (1 - e^{-k}),$$

therefore, equation (B 9) implies VB growth with

$$e^{-k} = 3/(3 + g) \text{ and } L_\infty (1 - e^{-k}) = 3h_1/(3 + g)$$

and therefore

$$k = \ln(1 + g/3) \tag{B 10}$$

and

$$L_\infty = 3h_1/g. \tag{B 11}$$

To derive  $t_0$ , equate the pre- and post-maturation growth curves when  $t = T$ . From equation (2.4),

$$L_T = h_1 (T - t_1)$$

and therefore

$$h_1 (T - t_1) = L_\infty (1 - e^{-k(T-t_0)}),$$

which solves to give

$$t_0 = T + \frac{1}{k} \ln(1 - g(T - t_1)/3). \tag{B 12}$$

Substituting for  $k$  (from equation (B 10)) gives

$$t_0 = T + \ln(1 - g(T - t_1)/3)/\ln(1 + g/3). \tag{B 13}$$

**APPENDIX C: OPTIMAL LIFE HISTORIES UNDER DETERMINATE GROWTH**

Assume that all surplus energy is allocated to somatic growth until age  $T$  then all net production is allocated to reproduction, with first spawning occurring at age  $T + 1$ . Energy available for reproduction in all breeding years  $= c W^{2/3} \propto L^2 \propto (h_1(T - t_1))^2$ . Therefore,

$$R_0 \propto \sum_{T+1}^{\infty} e^{-Mt}(T - t_1)^2 = \frac{e^{-M(T+1)} (T - t_1)^2}{1 - e^{-M}}$$

and, from this equation, the value of  $T$  that maximizes  $R_0$  is given by  $T - t_1 = 2/M$ , with the associated value of  $g = 3/(T - t_1) = 1.5M$ .

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.