



Biphasic growth in fish I: Theoretical foundations

Christopher Quince^{a,*}, Peter A. Abrams^a, Brian J. Shuter^{a,b}, Nigel P. Lester^{a,b}

^a Department of Ecology and Evolutionary Biology, 25 Harbord Street, University of Toronto, Toronto, Canada, ON M5S 3G5

^b Harkness Laboratory of Fisheries Research, Aquatic Research and Development Section, Ontario Ministry of Natural Resources, Peterborough, Canada, ON K9J 8M5

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ABSTRACT

We develop the theory of biphasic somatic growth in fish using models based on the distinction between pre- and post-maturation growth and an explicit description of energy allocation within a growing season. We define a 'generic biphasic' (GB) model that assumes post-maturation growth has a von Bertalanffy (vB) form. For this model we derive an explicit expression for the gonad weight/somatic weight ratio (g) which may either remain fixed or vary with size. Optimal biphasic models are then developed with reproductive strategies that maximise lifetime reproductive output. We consider two optimal growth models. In the first (fixed g optimal), gonad weight is constrained to be proportional to somatic weight. In the second (variable g optimal) model, allocation to reproduction is unconstrained and g increases with size. For the first of these two models, adult growth in a scaled measure of length has the exact vB form. When there are no constraints on allocation, growth is vB to a very good approximation. In both models, pre-maturation growth is linear. In a companion paper we use growth data from lake trout (*Salvelinus namaycush*) to test the bioenergetics assumptions used to develop these models, and demonstrate that they have advantages over the vB model, both in quality of fit, and in the information contained in the fitted parameters.

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1. Introduction

Size is an ecologically important property, influencing significant characteristics of individual organisms, such as fecundity, vulnerability to predators and availability of prey (Zivkov and Petrova, 1993; Persson et al., 1996; Lauer et al., 2005). For a large fraction of non-colonial marine and freshwater vertebrates and invertebrates (Andersen and Beyer, 2006), lifetime growth in body size is indeterminate (i.e. growth continues throughout adulthood but at a decelerating rate). Recent studies on a wide variety of aquatic species (e.g. vertebrates: sharks—Siegfried and Sanso, 2006; crocodiles—Tucker et al., 2006; salamanders—Leclair et al., 2006; invertebrates: speckled crab—Pinheiro and Hattori, 2006; bivalves—Cardoso et al., 2006; sea urchins—Kirby et al., 2006) have used the von Bertalanffy (vB) function as a simple description of indeterminate somatic growth patterns. This approach has been particularly common in studies of fish (e.g. Essington et al., 2001; Helser and Lai, 2004) where the vB function has been used for decades (e.g. Ricker, 1975). However, the usual energetic justification for this model is problematic. This justification holds that metabolic costs increase linearly with

weight, while energy intake follows an allometric function of weight, with an exponent less than one. Data on the relationship between weight and metabolic costs, summarised below, generally do not support the linear relationship. Furthermore, the traditional explanation for vB growth fails to account for the diversion of energy to reproduction at maturation (Day and Taylor, 1997) which, in female fish, typically exceeds 15% of somatic energy content annually (e.g. Shuter et al., 2005). Since the vB model does provide an accurate description of many fish growth patterns (Chen et al., 1992), it should be derivable from energetic and evolutionary principles. Furthermore, that derivation should provide insight into variation between species or populations in model parameters.

Several authors (Charnov, 1993; Day and Taylor, 1997; Lester et al., 2004), have recently suggested correcting the lack of an energetic cost of reproduction in the vB equation by using a biphasic growth curve, in which the somatic growth pattern prior to maturity has a functional form that differs from post-maturation growth. Biphasic growth in fishes has been discussed for nearly a century, with some of the early work reviewed by Iles (1974). In this paper, we develop an ecological and evolutionary model of body growth and reproductive investment in both immature and mature individuals of organisms characterised by indeterminate growth in a seasonal environment. This allows us to show why a variety of different models of growth result in approximately vB growth among adults. It also allows us to

* Corresponding author. Tel.: +44 141 330 8116; fax: +44 141 330 4557.

E-mail address: quince@civil.gla.ac.uk (C. Quince).

¹ Present address: Department of Civil Engineering, University of Glasgow, Glasgow G12 8LT, UK.

identify circumstances when a uniphase vB model is or is not a good approximate description of the lifetime growth trajectory. Finally, it shows why two previous models (Kozłowski, 1996; Lester et al., 2004), based on optimal age-specific energy allocations to reproduction, often produce similar predictions in spite of different assumptions about constraints on gonad size. While this study focuses on fish because information on fish growth is widely available, the models developed here could be of equal value in understanding the processes driving individual growth in other groups of animals with indeterminate growth.

The approach we adopt is essentially a simple dynamic energy budget (DEB) model (Kooijman, 1986, 1993; Nisbet et al., 2000, 2004; Lika and Kooijman, 2003). DEB models describe the changes in an individual's physiological state, in response to acquisition of energy from food and allocation of that energy to growth, maintenance or reproduction. Ours is a minimal bioenergetics model with only two state variables, somatic weight and gonad weight, and a small number of parameters (6) that can all be estimated from growth data. We also develop simpler models with fewer (4) parameters by assuming that allocation to reproduction maximises standard fitness measures. This simplification greatly aids in fitting the model to available data without sacrificing the underlying physiological mechanism. Another benefit of this combination of physiology and evolution is that the parameter estimates for the optimal growth models provide significant information on aspects of the ecological milieu that

typical population members experience (e.g. adult survival rate; size dependence of prey availability).

2. A uniphase model: generalised vB growth

The parameters used in this and subsequent models are defined in Table 1. The generalised vB model (Pauly, 1981) rests on the following assumptions: (i) energy assimilation rate is proportional to W^β , where W is body weight; (ii) metabolic costs are proportional to W ; (iii) W is proportional to L^3 , where L is body length. For all of our models, we will describe growth in terms of the 'size' variable v equal to $L^{3(1-\beta)}$. In the generalised vB model, it is v (not length) that has the standard exponential form:

$$v_t = v_\infty - (v_\infty - v_0) \exp(-kt), \quad (1)$$

where t is age in years, v_0 is the hypothetical size at age zero and v_∞ the maximum asymptotic size. Deriving this equation from energetics assumptions (Pauly, 1981) reveals that k is proportional to the metabolic cost coefficient and that a more natural parametrisation, which also has better fitting properties (Gallucci and Quinn, 1979), is to replace v_∞ with $h (= v_\infty k)$. Under this parametrisation, the generalised vB model has four parameters (v_0, h, β, k). To obtain lengths from Eq. (1) for fitting purposes we use the transformation $L_t = v_t^{1/3(1-\beta)}$. When we refer to growth having a vB form, it will mean that growth obeys Eq. (1).

Table 1
Variables and parameters defined in this paper

Subject	Symbol	Parameter	Defined by
Common variables	W	Somatic weight (g)	
	L	Length (mm)	
	G	Gonad weight (g)	
	\mathcal{P}	Net production (g days^{-1}) of somatic tissue	
	t	Age in years (yrs)	
	τ	Age in days (days)	
	D	Length of growing season (days)	
	Y	Length of year (days)	
Biphase framework	ζ	Production coefficient	$\mathcal{P}(W) = \zeta W^\beta$
	β	Production exponent	
	v	'Size' ($\text{mm}^{3(1-\beta)}$)	$v = (W/\Omega)^{1-\beta}$
	v_0	Initial size ($\text{mm}^{3(1-\beta)}$)	
	p_t	Proportion of season t devoted to somatic growth	
	h	Potential yearly increase in size ($\text{mm}^{3(1-\beta)}$)	$h = \zeta \Omega^{\beta-1} (1 - \beta) D$
	γ	Ratio of somatic to gonad wet weight energy densities	
	Ω	Somatic weight-length coefficient (g mm^{-3})	$W = \Omega L^3$
	g	Gonado-somatic index (GSI)	$g = G_t/W_t$
	g'	Energy weighted GSI	$g' = g/\gamma$
von Bertalanffy (vB) growth model	k	Rate of deceleration of growth	
Generic biphase model (age parameterised)	α	Initial invest. in somatic growth	$p_t = \alpha \chi^{t-(T+1)}$ if $t \geq T+1$
	χ	Rate of decay of p_t	$p_t = 1$ if $t < T+1$
	T	Last juvenile age	
Generic biphase model (size parameterised)	v_C	Intersect size	$p_t = \frac{v_\infty - v_t}{v_\infty - v_C}$ if $v_t \geq v_{T+1}$
	v_{T+1}	Maturation size	$p_t = 1$ if $v_t < v_{T+1}$
	v_∞	Asymptotic size	
Optimal strategies	s	Yearly survival probability	$s = \exp(-MY)$
	M	Instantaneous mortality (days^{-1})	
	o	Juvenile survival probability	
	w_e	Typical egg weight (g)	
	R_0	Expected no. of female offspring	
	r	Intrinsic rate of increase	

The original justification for the vB model made no reference to the costs of reproduction (von Bertalanffy, 1938). DEB theory assumes that these costs will be proportional to weight and apply to juveniles as well as adults, they can therefore be absorbed into the metabolic costs, generating vB growth curves given a constant food supply (Kooijman, 1986, 1993). Some subsequent models have assumed that, at maturity, a fixed fraction of body weight is invested into reproduction (e.g. West et al., 2001; Andersen et al., 2007). These models generate biphasic growth. However, their assumption of continuous reproduction leads to indeterminate growth if mortality is constant and reproductive allocation is optimised at each age (Kozłowski, 1996; Thygesen et al., 2005). Our model explicitly describes the sequence of changes in allocation expected within a year, when growth occurs in a seasonal environment. Under this framework evolutionary optimisation leads to biphasic, indeterminate growth.

3. Energetics framework for seasonal biphasic growth

Our framework for seasonal biphasic growth is based on the following set of assumptions:

1. Each year of Y days starts with a growing season lasting D days, followed by spawning, and then a period of zero growth of length $Y - D$ days corresponding to winter.
2. During the growing season, the net amount of energy available for tissue growth per day (\mathcal{P}), is an allometric function of somatic weight:

$$\mathcal{P}(W) = \zeta W^\beta, \quad (2)$$

where $W(\tau)$ is somatic weight at time τ (days). This differs from von Bertalanffy's assumption of different allometric exponents for consumption and metabolism. However, Eq. (2) is consistent with both interspecific (Peters, 1983) and intra-specific studies on the weight dependence of net production in fish (e.g. Ursin, 1979; Reiss, 1989) and other organisms. It is also consistent with the compendia of data provided in Hanson et al. (1997) on the weight dependence of maximum consumption and resting metabolic rate for 33 species of fish: both consumption and metabolic rate follow allometric functions of weight; mean values for the allometric exponents are 0.69 and 0.79, respectively; within a species, differences between the two exponents range from -0.418 to 0.03 , with an average of -0.1 . Given the relatively small differences in these two exponents, assuming a single exponent, β , is a useful simplification. The assumption that net production is a single power function of weight means that an organism could potentially grow to infinite size. This unrealistic outcome is prevented in practise by the increasing allocation to reproduction with increasing age. During winter $\mathcal{P}(W) = 0$.

3. For an immature organism, all energy available for growth is allocated to somatic tissue. For a mature organism, total weight at time τ can be divided into somatic and reproductive components ($W(\tau)$ and $G(\tau)$). At the start of a year, all available energy is allocated to somatic tissue growth. On completion of a fraction (p_t) of the growing season D (days), the organism switches to allocating all available energy to reproductive tissue growth. This discontinuous switch in allocation from somatic tissue to reproductive tissue has been shown to be optimal (Kozłowski and Teriokhin, 1999). On the D th day of year t ($\tau = tY + D$), the reproductive component is converted into sexual products. Therefore, both the somatic growth trajectory and lifetime reproductive output are determined by the proportions of each growing season devoted to somatic growth.

4. Somatic and gonad energy densities are assumed to be independent of size, but may differ from each other. Allometric dependence of somatic energy density on fish size (e.g. Stewart et al., 1983) can be included in Eq. (2), by changing the exponent of the scaling relation, but without changing its form and the validity of the following results. Measuring net production as rate of increase in somatic weight, the organism's somatic weight at the end of year t is

$$W_t = \int_{(t-1)Y}^{(t-1)Y+p_t D} \mathcal{P}(W(\tau)) d\tau + W_{t-1}, \quad (3)$$

where the gonad weight at spawning in year t is given by

$$G_t = \gamma(1 - p_t)D\mathcal{P}(W_t), \quad (4)$$

and γ is the ratio of the wet weight energy density of somatic tissue to gonad tissue.

Much of the literature on fish growth reports on the dynamics of length, rather than weight; this includes most formulations of the vB model. Our weight-based framework also provides a description of the dynamics of length because, for most species of fish (FishBase: <http://www.fishbase.org/>), length is approximately proportional to weight cubed ($W = \Omega L^3$). We now use the 'size' variable v , defined as in Section 2, by

$$v = (W/\Omega)^{1-\beta}.$$

This is equivalent to length if $\beta = \frac{2}{3}$, given the standard weight-length relationship. Differentiating v with respect to τ using the chain rule, and substituting for $dW/d\tau$ using Eq. (2), we find that $dv/d\tau$ is equal to a constant. Therefore size, v measured at the end of year t is a linear function of total time devoted to somatic growth:

$$v_t = v_0 + h \sum_{t'=1}^t p_{t'}, \quad (5)$$

where the constant h is given by

$$h = \zeta \Omega^{\beta-1} (1 - \beta) D.$$

This constant gives the annual increase in size of juvenile fish, and thus reflects the quality of the environment for growth. It is determined by both food availability and the energetic costs of obtaining that food. If we substitute Eq. (2) into Eq. (4), use the definition of h , and transform to v , then the gonad weight at the end of the growing season is

$$G_t = \frac{\gamma h \Omega}{1 - \beta} (1 - p_t) v_t^{\beta/1-\beta}. \quad (6)$$

Thus, a lifetime account of somatic growth and reproductive output follows directly from the lifetime allocation strategy $\mathbf{p} = (p_1, p_2, \dots, p_\infty)$. Within this general framework, Eq. (2) leads directly to juvenile growth that is linear in v ; however it does not prescribe a specific form for adult growth. We used two approaches to determine how this framework could yield vB growth: (i) we determined the set of allocations, \mathbf{p} , that generate the vB equation exactly; (ii) we assumed that the allocation strategy is determined by selection acting to maximise traditional fitness measures, and then determined if this was sufficient to yield vB growth.

4. Adult vB growth imposed: the generic biphasic (GB) model

Here we introduce a simple function for p_t that ensures vB growth post maturity. Let maturity occur at age $T + 1$, and the

proportion of the season devoted to growth at age $t \geq T + 1$, be given by

$$p_t = \alpha \chi^{t-(T+1)}, \quad (7)$$

where α gives the proportion of the growing season in the first adult year that is devoted to somatic growth, and χ measures the annual decrease of this proportion in the adult stage. Both parameters are restricted to lie between zero and one, $0 < \alpha < 1$ and $0 < \chi < 1$. When v is used to measure size, the growth pattern is given by

$$v_t = v_0 + ht, \quad t \leq T \text{ juvenile growth,}$$

$$v_t = v_\infty - (v_\infty - v_T) \exp(-k(t - T)) \quad t > T, \text{ adult growth,} \quad (8)$$

with $v_T = v_0 + hT$,

$$v_\infty = v_T + h\alpha/(1 - \chi), \quad (9)$$

and $\exp(-k) = \chi$. The growth strategy as a function of size is described by

$$p_t = 1, \quad v_t < v_{T+1}, \\ p_t = \frac{(v_\infty - v_t)}{(v_\infty - v_C)}, \quad v_t \geq v_{T+1}, \quad (10)$$

where

$$v_C = v_T + h(\alpha - \chi)/(1 - \chi). \quad (11)$$

This growth strategy is derived in Appendix A. We will refer to v_C as the ‘intersect size’ since it gives the size at which the two $p_t - v_t$ lines, describing the juvenile and adult strategies, intersect. The constraint $v_C < v_{T+1}$ arises from the conditions on α and χ . The life history is clearly biphasic, with linear growth before maturation, and vB growth, (as per Eq. (1)), afterwards. The allocation strategy can also be used to determine the gonad weights as a function of size at the end of each growing season, substituting Eq. (10) into Eq. (6), gives

$$G_t = \frac{\gamma h \Omega}{1 - \beta} \left(\frac{v_t - v_C}{v_\infty - v_C} \right) v_t^{\beta/(1-\beta)}, \quad (12)$$

for mature fish. The ratio of gonad weight to somatic weight (the gonado-somatic index) can be expressed as:

$$g = \frac{\gamma h}{(1 - \beta)(v_\infty - v_C)} \left(1 - \frac{v_C}{v_t} \right) \quad (13)$$

and thus g can either increase with size, remain fixed or decrease, according to whether v_C is >0 , 0 , or <0 , respectively. This generic biphasic (GB) model, is specified by six parameters, v_0 , h , β , T , α and χ . Growth curves generated by this model are shown in Fig. 1.

5. Constraints on reproductive investment generate adult vB growth

Lester et al. (2004) analysed a growth model that can be seen as a special case of the GB model. They used the empirical observation that the gonado-somatic index, g , is approximately constant in many species of fish to justify imposing a ‘fixed g ’ (FG) constraint on an energetics framework identical to that defined in Section 3. This is equivalent to a GB model with $v_C = 0$ and (from Eq. (13)):

$$v_\infty = \frac{h}{g'(1 - \beta)}. \quad (14)$$

By substituting Eqs. (11) and (14) into Eq. (9), and using the condition $v_C = 0$, we obtain

$$\chi \equiv \exp(-k) = \frac{1}{1 + g'(1 - \beta)}, \quad (15)$$

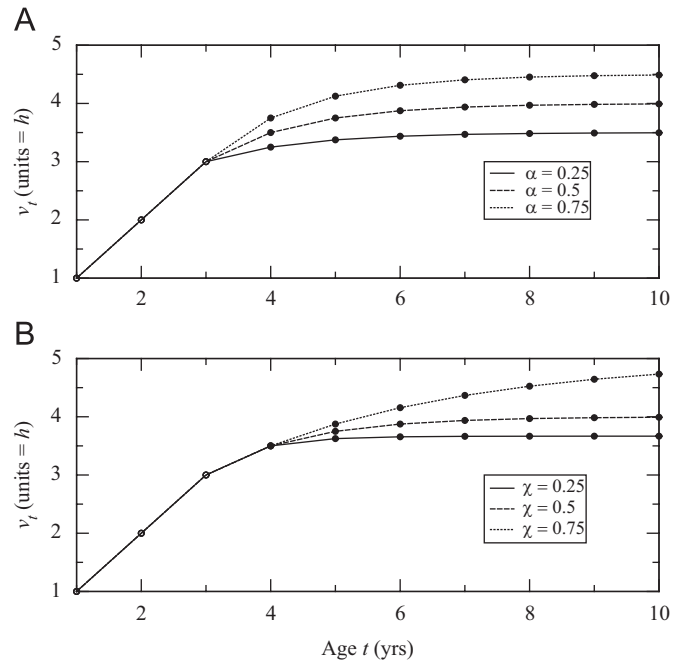


Fig. 1. The size v_t in units of h as a function of age (years) for the generic biphasic growth model. Parameters are $v_0 = 0$, $T = 3$ and in (A) $\chi = 0.5$ with $\alpha = 0.25, 0.5, 0.75$ and (B) $\alpha = 0.5$ with $\chi = 0.25, 0.5, 0.75$.

where we have absorbed the constant γ into a new constant $g' (= g/\gamma)$, the energy weighted gonado-somatic index. These expressions for v_∞ and k are generalisations to arbitrary β of results in Lester et al. (2004). The FG constraint simplifies the general GB structure, resulting in a five parameter growth model, (v_0, h, β, T, g') , that exhibits linear juvenile growth and vB adult growth. In what follows, we refer to this model as the FG model.

6. Optimal reproductive investment generates adult vB growth

An alternative approach to imposing vB growth through assumptions about model structure (GB model), or imposed constraints on parameters (the FG model), is to derive the adult growth curve from the assumption that evolution has shaped reproductive investment to maximise fitness. We will show that, for two standard fitness measures, this approach generates simple, four parameter models from our unconstrained, variable investment framework (see Section 3) that exhibit adult growth patterns that closely approximate a vB form.

6.1. Fitness measures

To proceed in this program, we adopt the following assumptions:

1. Fitness can be measured by R_0 (the expected number of female fish produced by a female over its lifetime) or r (the intrinsic rate of population increase). R_0 is the appropriate fitness measure for a population maintained at an equilibrium density by simple forms of density dependence while r is the appropriate fitness measure for a population without density dependence (Charlesworth, 1980; Mylius and Diekmann, 1995). We will focus our analyses on identifying those growth strategies that are consistent with R_0 maximisation. However, we will also show that there is a close linkage between these strategies and those arising from r maximisation.

2. Fecundity is proportional to gonad weight at the end of each growing season (Eq. (4)).
3. Mortality after some early age is constant throughout the year, independent of age and size and denoted by the annual survival probability s ($= \exp[-MY]$, where M (days⁻¹) is the instantaneous mortality rate).

Under these assumptions,

$$R_0 = \lambda \sum_{t=1}^{\infty} s^t (1 - p_t) D \mathcal{P}(W_t) \quad (16)$$

for a given strategy \mathbf{p} . The constant λ is given by $o\gamma/2w_e$, with γ being the ratio of somatic to gonad tissue wet weight energy density, w_e egg weight (assumed constant) and o the offspring survival probability, incorporating the mortality up to some early stage referred to above. We begin by demonstrating the similarity between strategies that maximise R_0 and strategies that maximise r . In our model, r is given by the characteristic equation,

$$\sum_{t=1}^{\infty} \exp(-rt) l(t) = 1, \quad (17)$$

where $l(t)$, the expected number of female offspring of age t attributable to a female born at time t years in the past, is given by,

$$l(t) = \frac{o\gamma s^t (1 - p_t) D \mathcal{P}(W_t)}{2w_e},$$

with somatic weight at each age W_t given by Eq. (3).

The necessary and sufficient condition for a life history to produce a local maximum in r is that the quantity $\sum_{t=1}^{\infty} \exp(-rt) l(t)$ be at a maximum, with r determined by Eq. (17) (Charlesworth, 1980). In our case this corresponds to maximising:

$$\lambda \sum_{t=1}^{\infty} \exp[-(r + M)t] (1 - p_t) D \mathcal{P}(W_t),$$

with the auxiliary equations (17) and (3). Comparing this to Eq. (16), it is clear that strategies that optimise r will be identical in form to the strategies that optimise R_0 , but with an adjusted mortality $r + M$, reflecting the non-zero growth of the population. This result depends on the lack of frequency dependence in the fitness of different types (Mylius and Diekmann, 1995), an assumption that is not satisfied in some other models of optimal reproductive allocation (Lika and Kooijman, 2003).

6.2. Maximising fitness: general net production

We now consider the lifetime allocation strategy $\mathbf{p} = (p_0, p_1, \dots, p_{\infty})$ that maximises R_0 without any constraints. This problem has been treated by Kozłowski (1996) using a slightly more general form for mortality. We will extend his results and place them in the context of our biphasic growth model. The strategy that maximises R_0 can be found by differentiating Eq. (16) with respect to p_t for each year t and setting the resulting equations equal to zero (Kozłowski, 1996). If some reproduction occurs, i.e. $p_t < 1$, then the optimum p_t obeys:

$$\mathcal{P}_t = (1 - p_t) D \mathcal{P}_t \mathcal{P}'_t + s \mathcal{P}_{t+1}, \quad (18)$$

where $\mathcal{P}_t = \mathcal{P}(W_t)$ and $\mathcal{P}'_t = \partial \mathcal{P} / \partial W$ evaluated at W_t . Eq. (18) represents a balance between the increase in R_0 associated with switching to reproduction on the left-hand side and the benefits of further somatic growth on the right. The first term on the right corresponds to the effect of increased size on reproductive potential this year and the second term encapsulates this effect

for all future years. If the following condition holds:

$$\mathcal{P}_t < s \mathcal{P}_{t+1}, \quad (19)$$

then $p_t = 1$ and all of year t is devoted to somatic growth.

By setting $p_t = 0$ in Eq. (18) we can find the maximum size, W_{∞} , which obeys:

$$\mathcal{P}'_{\infty} D = \frac{\partial \mathcal{P}}{\partial W}(W_{\infty}) D = (1 - s). \quad (20)$$

Trajectories can be determined by backwards recursion from a weight just slightly smaller than W_{∞} using what is effectively a dynamic programming approach. Given initial values for W_{t+1} and p_{t+1} we determine W_t by integrating weight backwards:

$$W_t = W_{t+1} + \int_{tY+Dp_{t+1}}^{tY} \mathcal{P}(W(\tau)) d\tau. \quad (21)$$

Then the optimum p_t obeys:

$$p_t = 1 - \frac{\mathcal{P}_t - s \mathcal{P}_{t+1}}{\frac{\partial \mathcal{P}}{\partial W_t} \mathcal{P}_t D}, \quad (22)$$

if $P_t \geq s P_{t+1}$ and $p_t = 1$ otherwise. The process can then be repeated to determine the entire growth trajectory.

For an arbitrary net production function, we conjecture that, provided $\partial \mathcal{P} / \partial W > 0$ and $\partial^2 \mathcal{P} / \partial W^2 < 0$, then $p_{t+1} < p_t$ once inequality (18) no longer holds. Thus, initially all production will be allocated to somatic growth until a threshold size is reached. Then increasing periods of time will be devoted to reproduction such that a maximum size is approached asymptotically.

6.3. Maximising fitness: allometric net production

We will now consider the unconstrained optimal growth curve under the assumption that net production is an allometric function of weight (Eq. (2)). Making our usual change of variables to size v , the above method for determining an optimal trajectory becomes a two-dimensional non-linear map backwards in time:

$$v_t = v_{t+1} - h p_{t+1},$$

$$p_t = 1 \quad \text{if} \quad \frac{v_{t+1}}{v_{t+1} - h p_{t+1}} > \left(\frac{1}{s}\right)^{1/\omega},$$

$$= 1 - \frac{(v_{t+1} - h p_{t+1})}{h \omega} \left[1 - s \left(\frac{v_{t+1}}{v_{t+1} - h p_{t+1}} \right)^{\omega} \right] \quad \text{otherwise,} \quad (23)$$

where $\omega = \beta / (1 - \beta)$. The first equation above arises because v is a linear function of the proportion of the season devoted to somatic growth (Eq. (5)) and the second is obtained from Eq. (22) after substituting Eq. (2) and transforming to v . This map has a fixed point at the maximum v :

$$v^* \equiv v_{\infty} = \omega h / (1 - s), \quad (24)$$

where $p^* = 0$.

Eqs. (23) determine optimum growth trajectories with no constraints, when given a final age and size. Usually we want to find a trajectory corresponding to a specified size at age zero (v_0). This is done by starting from an arbitrarily chosen size v_{\dagger} that is slightly smaller than v_{∞} . Below we describe how to find v_{\dagger} which will be close to zero in this region, using a linear stability analysis. We then iterate the map until v is smaller than v_0 . Given n as the number iterations required to do this, then age \dagger , associated with v_{\dagger} , is determined as $n - 1$. For any given v_{\dagger} we can, by iterating the map, determine the deviation between the predicted size at age zero, and the required value v_0 . We then solve numerically for the v_{\dagger} that makes this deviation zero. Because Eqs. (23) can be written as functions of the ratio v/h , and because size obeys Eq. (5), the timings of the annual switches from somatic growth to reproduction only depend on h through its effect on the initial

rescaled size v_0/h . This procedure defines a new growth model, based on four parameters (v_0, h, β, s), that we call the ‘variable g ’ optimal growth model (VGO).

6.3.1. The optimal switching strategy

A useful way to describe the growth curve in the case of an allometric net production is in terms of the optimal ‘switching strategy’ $p(v)$. This function gives the optimal proportion of the year devoted to somatic growth p_t as a function of size at the end of that year v_t . It can be determined numerically using Eq. (23). To obtain growth trajectories from $p(v)$ we integrate size through each season until the switching strategy is intersected. At that point allocation switches to reproduction and the size reached is the starting point for next year’s growth. In the vicinity of the fixed point, we can determine $p(v)$. We begin by performing a linear stability analysis near v_∞ , the details of which are given in Appendix B. It is easiest to do this in reversed time so that we start at the fixed point. The stability analysis reveals that one eigenvalue is greater than one (e_+) and one smaller than one (e_-). The fixed point is therefore a saddle. The larger eigenvalue is given by

$$e_+ = \frac{1}{2} \left(1 + s + \frac{1-s}{\omega} \right) \left(1 + \sqrt{1 - \frac{4s}{\left(1 + s + \frac{1-s}{\omega} \right)^2}} \right). \tag{25}$$

All optimum growth trajectories will asymptotically approach the fixed point along the separatrix with eigenvalue greater than one (e_+), because in forward time this will be the stable separatrix. Consequently, in the vicinity of the fixed point, $p(v)$ is given by the eigenvector corresponding to this eigenvalue:

$$p(v) = [e_+ - 1] \frac{(v_\infty - v)}{h}. \tag{26}$$

The optimal strategy in the vicinity of the asymptotic size is a linearly decreasing function of v , and, just as in our formulation of the GB model (see Eqs. (10)) this leads to an optimal trajectory with a vB form:

$$v_t = v_\infty + (v_l - v_\infty) \exp(-\ln(e_+)[t - l]),$$

where l is sufficiently large that v_l is close enough to v_∞ for the linear approximation to be valid.

The linear stability analysis gives us insight into how the parameters of the VGO model affect the maximum size and the rate at which it is approached. From Eqs. (24) and (25) we see that increasing h will increase v_∞ but not change the rate at which it is approached. Increasing β increases v_∞ but decreases e_+ and the rate at which the asymptotic length is reached. Increasing β also increases the observed growth, presumed to be length as $L_t = v_t^{1/3(1-\beta)}$. The effect of increased survival s is to increase v_∞ .

Numerical investigation reveals that $p(v)$ is not only linear near v_∞ , but that this holds to a good approximation over the whole range of v for which $p(v) < 1$. Fig. 2 gives the optimal switching strategies at fixed s for three different values of β . The relationships are approximately linear and approach Eq. (26) as $v \rightarrow v_\infty$ for all values of β . In general if we denote v_C as the point at which $p(v_C) = 1$, then the straight line approximation to $p(v)$ is

$$\hat{p}(v) = \frac{v_\infty - v}{v_\infty - v_C}. \tag{27}$$

Consider Eqs. (23) when $\beta = \frac{1}{2}$, in this case the equations are linear and the approximation holds exactly. We can determine v_C by comparing Eq. (27) with Eq. (26) and substituting Eq. (25):

$$v_C = h \left[\frac{1}{1-s} - \frac{1}{\sqrt{1-s}} \right],$$

a monotonically increasing function of s .

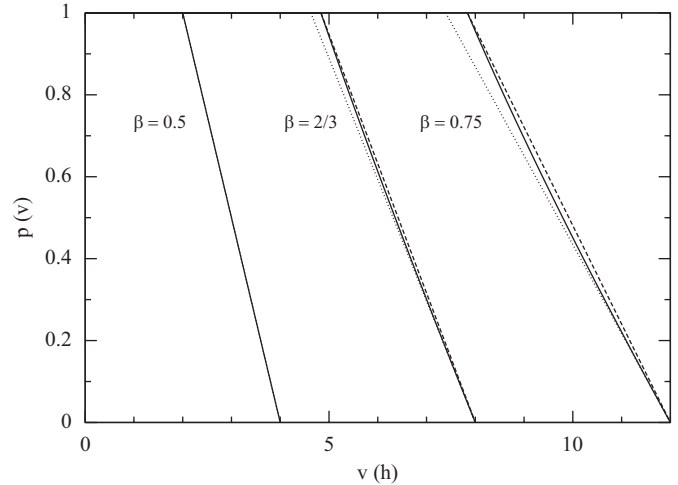


Fig. 2. The optimal switching strategies $p(v)$ (solid lines), for $s = 0.75$ and $\beta = 0.5, \frac{2}{3}, 0.75$. The tangents to the curves at v_∞ given by Eq. (26) are shown as dotted lines and the straight line approximations $\hat{p}(v)$ given by Eq. (27) as dashed lines.

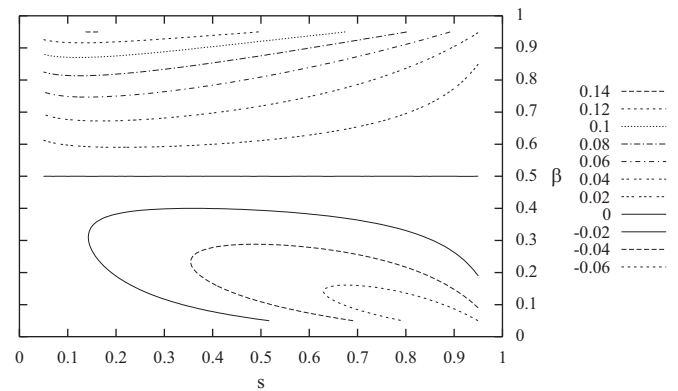


Fig. 3. The minimum (maximum) value of $\hat{p}(v) - p(v)$ when $\beta < 0.5$ ($\beta > 0.5$) over the full range $v_C \leq v \leq v_\infty$ as a function of s and β .

Numerical results show that when $\beta < \frac{1}{2}$, $p(v)$ is always greater than $\hat{p}(v)$ and when $\beta > \frac{1}{2}$, $p(v)$ is always smaller than $\hat{p}(v)$. The deviations are never large for β values in the empirically observed range. This is illustrated in Fig. 3 where we show the minimum (maximum) value of $\hat{p}(v) - p(v)$ when $\beta < 0.5$ ($\beta > 0.5$) over the full range $v_C \leq v \leq v_\infty$ as a function of s and β (note that this is independent of h). Realistic s and β values both fall around 0.7 for which the maximum deviations are less than 4%. In addition when $\beta > 0.5$ these deviations will not accumulate along a trajectory.

The linear form for the switching strategy equation (27) only holds when $v \geq v_C$; otherwise all excess production is allocated to somatic growth ($p_t = 1$). For general β , we determine v_C numerically as the size for which $v_{t+1}/v_t = (1/s)^{1/\omega}$. Combining these two components, the complete switching strategy given our approximation is then ‘piece-wise’ linear:

$$p(v) = 1, \quad v < v_C, \\ p(v) \simeq \frac{v_\infty - v}{v_\infty - v_C}, \quad v \geq v_C. \tag{28}$$

If the switching strategy is a linearly decreasing function of size, as it is for adults in Eqs. (28), then growth will have the vB form. Consequently to a good approximation the optimal growth curves are described by the GB model (Eqs. (8)), with linear growth in size before maturation and vB growth after maturation. This is illustrated by Fig. 4. However, we now have the restriction $v_C > v_T$,

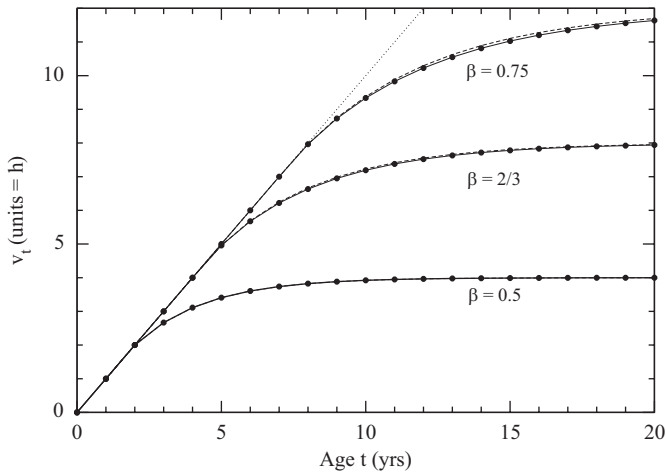


Fig. 4. Example VGO v_t trajectories (solid lines and black dots) in units of h for $s = 0.75, v_0 = 0$ and $\beta = 0.5, \frac{2}{3}, 0.75$. The variable v ‘size’ is a transformed function of weight, $v = (W/\Omega)^{1-\beta}$, such that $v_t = v_0 + h \sum_{t=1}^t p_t$. Dashed lines are the generic biphasic model approximations (Eqs. (8)) with parameters determined from Eq. (28). Note that the optimum trajectories and their approximations lie nearly on top of each other. The dotted line gives $v_t = t$ to illustrate when maturity occurs.

because maturation occurs in the first year that the final size is greater than v_c . As a result v_c must be greater than zero and g will increase with size.

We have focused on the optimal strategy when net production is an allometric function of weight, but as discussed in Section 2 a more general form for the net production would be to have two allometric terms, corresponding to the assimilation rate minus the metabolic costs. That results in a unimodal net production with a maximum at W_{max} . In Appendix C, we consider the optimal strategy for this case, and show that growth ceases before net production reaches its maximum ($W_\infty \leq W_{max}$) and that provided ($W_\infty \ll W_{max}$) the resulting growth curves can be approximated by the VGO model.

6.4. Maximising fitness: the FG model

In the following sections, we will find it useful to compare the performance of the VGO model with a version of the FG model that incorporates the assumption that selection has maximised lifetime reproductive investment. We call this model the fixed g optimal growth model (FGO). To derive the FGO model, we need an expression for R_0 . By noting that, under the FG model, the gonad weight at the end of each season is equal to gW_t , weighting this by the probability of surviving to spawn s^t , transforming to size v_t and substituting from Eqs. (8) with $v_c = 0$, we get:

$$R_0 = \lambda \Omega g^T s^T \sum_{t=T+1}^{\infty} s^{t-T} [v_\infty - (v_\infty - v_T) \exp(-k(t-T))]^{1-\beta}, \quad (29)$$

where from Eq. (15), k is a simple function of g' and β . For a set of feasible values for v_0, h, β and s , numerical investigation shows that there is a unique pair of values for g' and T that maximises R_0 . This pair of values defines the optimum reproductive allocation strategy embodied in the FGO model. The FGO model is parameterised by the same four parameters (v_0, h, β, s) that define the VGO model. It also shares with the VGO model the property that the allocation strategy is a function of $v_0/h, s$ and β only. This occurs because the optimum strategy depends only on the summation term in Eq. (29) and h factors out of that term leaving it dependent only on the ratio v_0/h .

7. Behaviour of optimal allocation strategies

Both the VGO and the FGO models exhibit expected (Abrams and Rowe, 1996; Day and Taylor, 1997; Lester et al., 2004) responses to increased survival probability: delayed maturation and decreased investment in reproduction post-maturation. This is shown for the FGO model in Fig. 5A where T increases and g' decreases with increasing s . The effect of β on maturation and investment in reproduction is similar to that of s for both models (illustrated for the FGO model in Fig. 5B): increasing the production scaling exponent favours somatic growth over reproduction. Despite similar qualitative behaviour, the FGO and VGO models differ substantially in the maturation sizes and asymptotic sizes they predict for given values of s and β (Fig. 6). Asymptotic and maturation sizes increase with survival probability for both models but under the VGO model, fish have smaller asymptotic

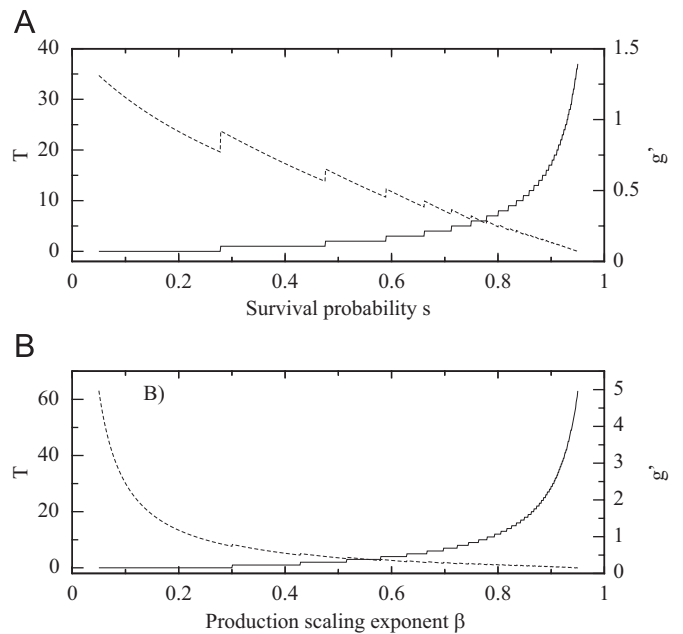


Fig. 5. (A) Optimal T and g' values in the FGO model as a function of s for $\beta = \frac{2}{3}$. (B) Optimal T and g' values in the FGO model as a function of β for $s = 0.75$. In both graphs the solid line gives T and the dashed line g' .

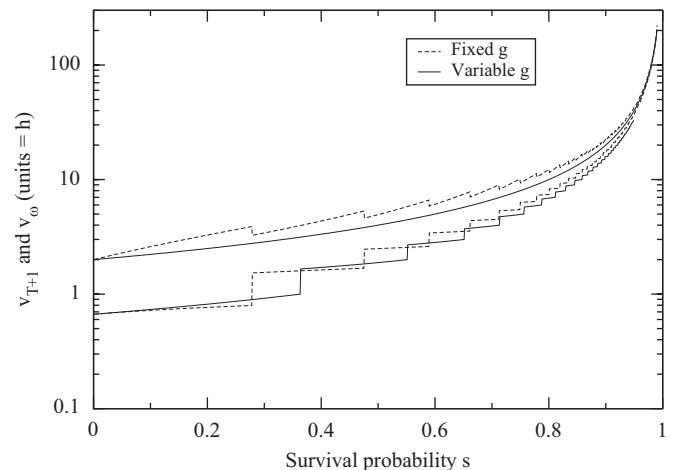


Fig. 6. v at maturation (v_{T+1}) and the asymptotic value v_∞ in units of h for the fixed g (dashed lines) and variable g (solid lines) optimum growth models as a function of s for $\beta = \frac{2}{3}$. For both models the upper line corresponds to v_∞ .

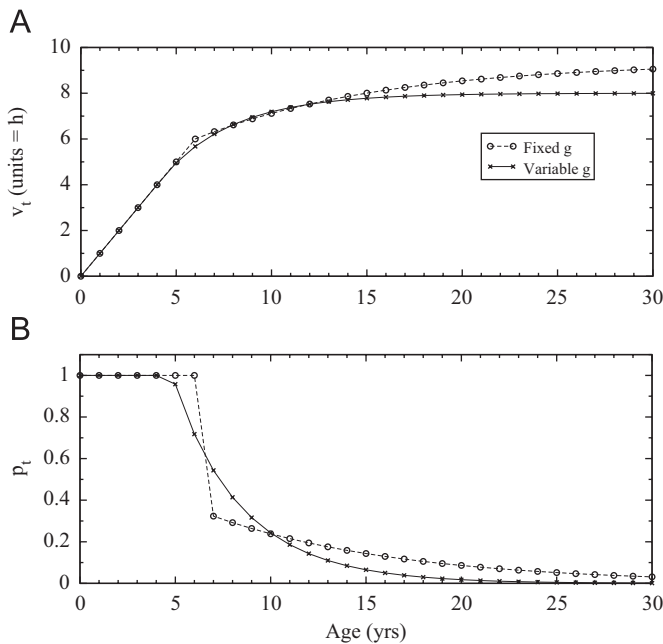


Fig. 7. (A) Example growth trajectories showing 'size' v_t in units of h as a function of age in years for the VGO (solid black line with crosses) and FGO (dashed black line with open circles) models. (B) Proportion of year devoted to somatic growth p_t as a function of age for these growth trajectories. Both trajectories have parameters ($s = 0.75$, $v_0 = 0$, $\beta = \frac{2}{3}$) so in this case $v = L$.

sizes and, unless s is small, mature at a smaller size. Asymptotic and maturation sizes also increase with β at fixed s for both models. In the VGO model we have an explicit expression for the asymptotic size (Eq. (24)) from which the dependence on s and β can be directly determined. When we compare (Fig. 7) the FGO and VGO growth trajectories and optimal allocation strategies, we see that the VGO strategy invests more in reproduction both earlier and later in life than the FGO strategy. The FGO strategy is forced, by the fixed g constraint, to begin reproductive allocation later in life with an abrupt shift of resources to a level that initially exceeds that exhibited by the VGO strategy. Over time, the gradually increasing VGO allocation level reaches and exceeds the fixed level predicted by the FGO model. It is important to note that, at any point in parameter space, the maximum fitness R_0 under the FGO model is only slightly less ($\approx 1\%$) than that of the VGO model, for typical values of s and β .

8. Discussion

In this study, we introduced a general framework for seasonal biphasic growth models based on simple energetics arguments. Using this general framework, we developed the generic biphasic model. This model should be viewed as an alternative to the von Bertalanffy growth model, to be applied to seasonally reproducing species whose growth pattern is significantly altered by sexual maturity. Its parameters quantify not only the organism's growth but also its energy allocation strategy. Our work generalises and extends findings presented in a variety of earlier studies (Charnov, 1993; Kozłowski, 1996; Day and Taylor, 1997; Lester et al., 2004).

The generic biphasic model does not explain why growth post-maturation should have a vB form. We explored two hypotheses that produce post-maturation vB growth. Firstly, if the ratio of gonad weight to somatic weight (gonado-somatic index g) is constrained to be constant throughout the adult period (FG model), then post-maturation growth is of the vB type. Secondly, if g is unconstrained but growth is optimal in the sense of

maximising either of the two standard measures of fitness (R_0 —lifetime reproductive output, or r —intrinsic rate of population increase) given a fixed survival probability (VGO model), then growth post-maturation has a form that closely approximates vB growth. The former had been noticed previously in a less general context by Lester et al. (2004), while the optimal growth model has also been studied previously (Kozłowski, 1996). We extended these works by deriving the limiting form of the associated somatic growth pattern near the asymptotic size, and the complete growth pattern for $\beta = 0.5$. We showed that post-maturation growth approximates the generalised vB form for reasonable values (0.5–0.8) of β and that this result is independent of the fitness measure (r or R_0) maximised. This clarifies the earlier finding of Czarnoleski and Kozłowski (1998), that optimal growth generates lifetime growth curves that have an approximately von Bertalanffy form, by showing that this is only true for adult growth and that it arises out of the approximately linear form for the optimal switching strategy.

The VGO model and the FGO model both depend on the same four parameters: the initial size v_0 , the annual increase in size of pre-reproductive individuals h , the growth exponent β , and the yearly survival probability s . Both models respond to variation in these parameters in essentially the same way. The initial size v_0 , shifts the starting point of the growth curves, while h scales all sizes, leaving the timings of the switches from somatic growth to reproduction essentially unchanged. The two parameters that significantly impact the growth strategies are s and β an increase in either favours somatic growth, delays the timing of maturation and results in larger asymptotic sizes. The effects of increased survival have been observed in other life history models (Charnov, 1993; Abrams and Rowe, 1996; Day and Taylor, 1997), but the similar effects of β have not been noted previously. For the same parameter values, maturation and asymptotic sizes are smaller in the VGO model. In addition, g at first spawning is smaller than in the comparable FGO model, but it reaches a higher value later in life.

Of course, all models are simplifications of nature, and a variety of factors we have not considered here may have some effect on the outcome of the analysis. We have ignored between-individual variation in environmental and genetic factors affecting growth. Food supplies have been assumed to be constant, and there is no representation of the dynamics of specific food items. Potential somatic growth is a simple allometric function of weight, however, our analysis (Appendix C) of the optimum growth curves that result under separate intake and loss functions shows that this is a reasonable approximation given the relatively small differences in exponents documented by Hanson et al. (1997). Mortality and food supplies are assumed to be independent of time, size, and age. The simple life-history optimisation approach assumes a constant environment and no genetic constraints on achieving the optimum. In some cases, there are biological reasons for suspecting that some of these modifying factors are likely to have small effects. For example, the potential reduction in mortality due to larger size in older adults is likely to be offset by the increases due to senescence. It may be that many of the potential additional details will not greatly alter our results. For example, Jørgensen and Fiksen (2006) using a complex optimum allocation model incorporating metabolism, migration and stochasticity obtained a pattern of increased allocation to reproduction and decelerating adult growth qualitatively similar to the growth curves we derive. A long series of analyses suggest that increased reproductive investment with increased age is likely to be a common feature of life histories (Roff, 2002). Such a pattern is likely to produce a pattern of decelerating growth in any adult organism with a limited food supply or a limited capacity to convert food into new biomass.

The new models we present in this paper provide a link between descriptive models used for curve fitting and detailed energetics models that explicitly incorporate some, or all, of the biological complexities listed above. In a companion paper (Quince et al., 2008), we test our simple models in a variety of ways using field and laboratory data from over 20 independent populations of lake trout (*Salvelinus namaycush*), a large freshwater top predator. We show that our simple models provide superior descriptions to the vB model of somatic growth patterns observed in wild populations and that the survival probabilities predicted by these fitted growth curves correspond with independent estimates of the survival probabilities experienced by those populations. These correspondences between model predictions and observed behaviour of fish in the wild suggest that the simplifications we have made in constructing our models may have relatively modest effects on their ability to capture significant aspects of the growth and dynamics of real individuals and populations.

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Appendix A. Derivation of growth strategy as a function of size

For sizes smaller than the size at maturation v_{T+1} , $p_t = 1$, because the entire season is devoted to somatic growth. For larger sizes Eq. (7) holds. Rearranging the second line of Eqs. (8) and using the relation $\exp(-k) = \chi$, gives

$$\frac{v_\infty - v_t}{v_\infty - v_T} = \chi^{t-T}.$$

Substituting this into Eq. (7) and using the expression $v_\infty = v_T + h\alpha/(1 - \chi)$, we have

$$p_t = \frac{(v_\infty - v_t)}{\frac{h\chi}{1 - \chi}}.$$

Finally defining $v_C = v_T + h(\alpha - \chi)/(1 - \chi)$ this can be rewritten as:

$$p_t = \frac{(v_\infty - v_t)}{(v_\infty - v_C)},$$

which holds for $v_t \geq v_{T+1}$.

Appendix B. Linear stability analysis near v_∞

In this appendix we detail the linear stability analysis near the fixed point of the 2D non-linear map defined by Eqs. (23). The fixed point occurs at (p^*, v^*) where $p^* \equiv 0$ and $v^* \equiv v_\infty$. The asymptotic size is given by Eq. (24). Changing variables in Eqs. (23) ($x_t = (v_t - v^*)/h$, $y_t = p_t$) and reversing time gives

$$\begin{aligned} x_{t+1} &= x_t - y_t, \\ y_{t+1} &= 1 - \frac{(x_t + \eta - y_t)}{\omega} \left[1 - s \left(\frac{x_t + \eta}{x_t + \eta - y_t} \right)^\omega \right], \end{aligned}$$

with $\eta = v^*/h = \omega/(1 - s)$. Here we have assumed that near the fixed point $p_t < 1$.

Linearising these transformed equations:

$$\begin{pmatrix} \Delta x_{t+1} \\ \Delta y_{t+1} \end{pmatrix} = \begin{pmatrix} 1 & -1 \\ -\frac{1-s}{\omega} & s + \frac{1-s}{\omega} \end{pmatrix} \begin{pmatrix} \Delta x_t \\ \Delta y_t \end{pmatrix},$$

where Δ indicates that x_t and y_t are sufficiently small to ignore higher order terms.

The Jacobian has two eigenvalues:

$$e_{\pm} = \frac{1}{2} \left(1 + s + \frac{1-s}{\omega} \right) \left(1 \pm \sqrt{1 - \frac{4s}{\left(1 + s + \frac{1-s}{\omega} \right)^2}} \right).$$

The parameters are restricted to $0 \leq s < 1$ and $0 \leq \omega < \infty$. Thus both eigenvalues are always real since $4s < (1 + s + (1 - s)/\omega)^2$. The larger eigenvalue e_+ is greater than one since it is a monotonically decreasing function of ω and $e_+ \rightarrow 1$ in the limit $\omega \rightarrow \infty$. Plotting e_- as a function of ω and s reveals $0 < e_- < 1$. The fixed point is therefore a saddle.

Appendix C. Optimal growth with an unimodal net production

As discussed in Section 3, a more detailed description of a fish's energetics is to use a net production with separate allometric functions for assimilation and metabolic costs:

$$P(W) = \alpha W^\beta - \gamma W^\delta,$$

with $\beta < 1$ and $\beta < \delta$. This will result in a unimodal net production with a derivative $\partial P/\partial W$ that decreases monotonically from ∞ when $W \rightarrow 0$, and is equal to zero at the weight that maximises net production, $W_{max} = [\alpha\beta/\gamma\delta]^{1/(\delta-\beta)}$.

It is harder to analyse the optimum growth trajectory in this case than for a single allometric function. The asymptotic weight W_∞ will be determined by Eq. (20). This equation states that growth ceases when $\partial P/\partial W$ is equal to $(1 - s)/D$, a positive value that approaches zero as survival probability approaches one. Therefore there is a single solution for W_∞ , that is an increasing function of survival probability, and this asymptotic weight is always smaller than or equal to W_{max} , with equality when $s = 1.0$. The optimum strategy is always to asymptote to a size smaller than that at maximum production. The actual value of W_∞ must be determined numerically.

The complete optimum trajectory can also be derived for this production function using Eq. (22) and integrating weight backwards, Eq. (21). As discussed in Section 3 there is evidence that $\delta - \beta$ is small and for typical survival probabilities this leads to an asymptotic weight which is much smaller than the weight at maximum production, $W_\infty \ll W_{max}$. We have shown numerically that in this case the optimum allocation strategy generates age-length curves indistinguishable from those produced by a single allometric function, i.e. the VGO model, but with an exponent that is smaller than β —over the realised range of sizes the unimodal net production can be approximated by a single allometric function. For parameter values where W_∞ approaches W_{max} then the optimum allocation strategy shows a rapid switch from somatic growth to allocation to reproduction, and an abrupt flattening-off in growth at maturation results. These curves cannot be approximated by the VGO model, but this growth pattern does not correspond to the many years of indeterminate growth typically observed in long lived seasonally reproducing fish.

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