Abstract—We propose an extended form of the von Bertalanffy growth function (VBGF), where the allocation of surplus energy to reproduction is considered. Any function can be used in our model to describe the ratio of energy allocation for reproduction to that for somatic growth. As an example, two models for energy allocation were derived: a step-function and a logistic function. The extended model can jointly describe growth in adult and juvenile stages. The change in growth rate between the two stages can be either gradual or steep; the latter gives a biphasic VBGF. The results of curve fitting indicated that a consideration of reproductive energy is meaningful for model extension. By controlling parameter values, our comprehensive model gives various growth curve shapes ranging from indeterminate to determinate growth. An increase in the number of parameters is unavoidable in practical applications of this new model. Additional information on reproduction will improve the reliability of model estimates.

A note on the von Bertalanffy growth function concerning the allocation of surplus energy to reproduction

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The von Bertalanffy growth function (VBGF) has been used to analyze somatic growth data in a wide range of studies. It is now commonly put into practice to partially reparameterize the VBGF parameters to avoid their covariation and to ensure statistical accuracy (Quinn and Deriso, 1999).

Although variations in the growth rate influenced by extrinsic environmental fluctuations have been examined in many studies, we propose that intrinsic physiological dynamics are also of great importance. The interaction between growth rate and sexual maturation has often been debated in life history studies (Roff, 1984; Beverton, 1992; Jensen, 1996). Mathematical treatments for representing the switch in energy allocation between growth and reproduction have been introduced to discuss optimal life-history strategies (Roff, 1983; Kozłowski, 1992, 1996; Kozłowski and Teriokhin, 1999). When the energy budget of fishes has been quantified, dynamics of the energy distribution between growth and reproduction have often been considered in simulated scenarios (Jørgensen and Fiksen, 2006; Pecquerie et al., 2009).

The effects of reproductive energy should also be important for practical curve fitting studies. A biphasic growth model derived by connecting two independent VBGFs at an arbitrary age is often employed for curve fitting (Soriano et al., 1992; Porch et al., 2002; Araya and Cubillos, 2006; Quince et al., 2008a, 2008b; Alós et al., 2010; Tribuzio et al., 2010). Although a biphasic VBGF is one approach used to account for inflections in growth and is similar to the higher-parameter model (Schnute and Richards, 1990), results of model selection based on the Akaike information criterion (AIC; Akaike, 1973) often indicate that the biphasic VBGF is a more suitable model than the original monophasic VBGF (Porch et al., 2002; Araya and Cubillos, 2006; Tribuzio et al., 2010). The better fit implies that the delay in growth due to a reallocation of energy may be detected as a change in the growth trajectory.

Day and Taylor (1997) and Czarnołęski and Kozłowski (1998) identified the lack of an explicit formula for the reproductive process in the VBGF. Although the biphasic VBGF is an empirical approach, a deductive model that can incorporate both growth and reproduction should be developed to help to understand the process of energy allocation and to improve curve fit. In this study, we begin with an extension of the VBGF with respect to a continuous change in energy allocation. We also present an application of curve fitting and model selection. An overview of changes in growth-curve shapes is subsequently shown. Finally, we briefly discuss the features of our model.

Methods

We start with the general form of VBGF given by

$$\frac{dw}{dt} = hw^{2/3} - kw, \qquad (1)$$

where w, t, h, and k are body weight, age, and coefficients of anabolism and catabolism, respectively. The right hand side of Equation 1 is the total production rate of surplus energy.

If we consider the reallocation of surplus energy for reproduction, Equation 1 can be expanded as

$$\frac{dw}{dt} + c\frac{df}{dt} = hw^{2/3} - kw. \qquad (2)$$

Two newly introduced terms, f and c, denote the cumulative energy investment for reproduction until age t and the conversion factor of reproductive energy to body weight, respectively. Note that f is not equivalent to the weight of the gamete (i.e., eggs or spermatozoa). Equation 2 is equivalent to the exoskeleton growth model (Ohnishi and Akamine, 2006) in that energy allocation to activities or appendages unrelated to somatic growth are explicitly described.

Suppose $w = \beta l^3$, where l is body length and β is a constant proportionality coefficient. Dividing $dw/dt = 3\beta l^2 dl/dt$ by each side of Equation 2 and substituting $w = \beta l^3$ yields the following equation:

$$\frac{dl}{dt} = \left(\frac{dw}{dt}\right)\left(\frac{dw}{dt} + c\frac{df}{dt}\right)^{-1} K\left(l_\infty - l\right), \qquad (3)$$

where $K = k/3$ and $l_\infty (= hk^{-1}\beta^{-1/3})$ is the asymptotic length. Let p be the ratio ($0 \le p \le 1$) of energy invested to reproduction against total surplus energy such that

$$p = \left(c\frac{df}{dt}\right)\left(\frac{dw}{dt} + c\frac{df}{dt}\right)^{-1}. \qquad (4)$$

Hence, Equation 3 becomes

$$\frac{dl}{dt} = (1-p)K\left(l_\infty - l\right). \qquad (5)$$

Equation 5 comprehensively describes two types of life history strategies, which can be generally classified as determinate and indeterminate growth (Lincoln et al., 1998). It tends towards determinate growth when p is close to 1.0 and otherwise towards indeterminate growth. The value of the parameter p increases with sexual maturation, and it can be replaced by $p(w)$, $p(l)$, or $p(t)$ as a function of size or age. In particular, a mathematical treatment is easy when $p \equiv p(t)$. Given that $l=0$ at $t=t_0$ (the initial condition), the general form of the growth function is given as

$$l = l_\infty\left(1 - e^{-K \cdot T(t)}\right), \text{ where } T(t) = \int_{t_0}^{t}\left\{1 - p(s)\right\}ds. \qquad (6)$$

It should be noted that $p(t)$ can take an arbitrary functional form with $0 \le p(t) \le 1$.

Among the various possible forms of $p(t)$, we propose the following two models that are relatively easy to derive. The first is a model where $p(t)$ exhibits a discontinuous change in age at maturity t_m, such that $p(t)=0$ ($t<t_m$) and $p(t)=v$ ($t \ge t_m$), where $0 \le v \le 1$. In this case, $T(t)$ is defined by

$$T(t) = \begin{cases} t - t_0 & (t < t_m) \\ t - t_0 - v(t - t_m) & (t \ge t_m) \end{cases}. \qquad (7)$$

Equation 7 represents the time delay to attain a certain body size in $t \ge t_m$ due to change in energy allocation. Consequently, the growth curve becomes biphasic, combining two independent VBGFs.

The alternative model assumes that $p(t)$ changes continuously throughout an individual's lifetime. In particular, an S-type curve that has an inflection point around $t=t_m$ is suitable for describing a change in $p(t)$ due to sexual maturation. Let $p(t)$ be $p(t)=v/(1+\exp(-a(t-t_m)))$ as a general logistic curve such that the analytical solution for $T(t)$ is given by

$$T(t) = (1-v)(t-t_0) - \frac{v}{a}\left\{\log\left(1 + e^{-a(t-t_m)}\right) - \log\left(1 + e^{-a(t_0-t_m)}\right)\right\}, \qquad (8)$$

where v and a are the upper limit of the allocation rate in reproductive energy and the rapidity of maturation, respectively. The logistic function converges to a step-function when $a \to \infty$. By inspection, Equation 7 is a special case of Equation 8.

The solution for Equation 5 is complicated when $p \equiv p(l)$ (or $p \equiv p(w)$) such that

$$\int_0^l \frac{1}{(l_\infty - x)(1 - p(x))}dx - K(t - t_0) = 0. \quad [0 \le p < 1] \qquad (9)$$

The explicit solution for l is a biphasic VBGF when $p(l)$ is a step-function that has discontinuous switching at

Table 1

Parameter estimates for two types of von Bertalanffy growth functions (VBGFs). Both types of VBGF have three common parameters: asymptotic length (l_∞), growth coefficient (K), and initial condition of age (t_0). Additional parameters, namely age at maturity (t_m), the upper limit of the allocation rate in reproductive energy (v), and rapidity of maturation (a), were used in the extended model. Values within parentheses show the square root of the variance of the estimates derived from the matrix inverse of the Hessian matrix. The ΔAIC shows the relative difference of the Akaike information criterion (AIC) value compared with the minimum AIC.

Type of VBGF	l_∞	K	t_0	t_m	v	a	AIC	ΔAIC
Conventional model	260.72	0.34	−0.45	—	—	—	26881.3	20.8
	(1.51)	(0.01)	(0.04)					
Extended model	463.01	0.15	−0.77	3.41	0.79	1.01	26860.5	0
	(49.08)	(0.01)	(0.14)	(0.35)	(0.05)	(0.21)		

the boundary of mature "size." In most cases, however, it is not easy to obtain an explicit solution, as shown in Equation 6, owing to the complexity of the integrand in Equation 9.

Allocated reproductive energy can be derived as follows by rearranging Equation 4 with the condition $p \equiv p(t)$ as

$$\left(1 - p(t)\right) c \frac{df}{dt} = p(t) \frac{dw}{dt}.$$

Substituting $dw/dt = 3\beta l^2 dl/dt$ and Equation 5 into this equation, one obtains

$$\frac{df}{dt} = \frac{3\beta K}{c} p(t) l^2 \left(l_\infty - l\right), \qquad (10)$$

$$f = \frac{3\beta K}{c} \int_{t_0}^{t} p(s) l^2 \left(l_\infty - l\right) ds. \qquad (11)$$

Equation 10 represents the instantaneous reproductive energy at age t. Equation 11 shows the cumulative investment of reproductive energy until age t. Thus, changes in two quantities (body size in Eq. 6 and energy investment in Eq. 10) are treated in an extended VBGF.

We fitted the growth curve in Equations 6 and 8 to individual measurements in length-at-age as $L_i (i=1,...,N)$, where N is the total number of samples. Parameters were estimated by minimizing the residual sum of squares of $S = \sum_i (L_i - l_i)^2$. The numerical optimization for S was accomplished by using the quasi-Newton method (BFGS algorithm) in "optim( )" with R statistical software (R Development Core Team, 2011). The comparison between this model and the original monophasic VBGF was based on the AIC value as follows: AIC=Nlog$S$+2θ, where θ is the number of free parameters.

We used measurement data on willowy flounder (*Tanakius kitaharai*) males collected by bottom-trawl surveys in the coastal area of Fukushima Prefecture, Japan, from 2004 to 2006. The sample size was n=2169. Age ranged from 1.38 to 14.30 years and length ranged from 113 to 298 mm (standard length). Otoliths were used to determine yearly ages and dates of birth were assigned as January 1st.
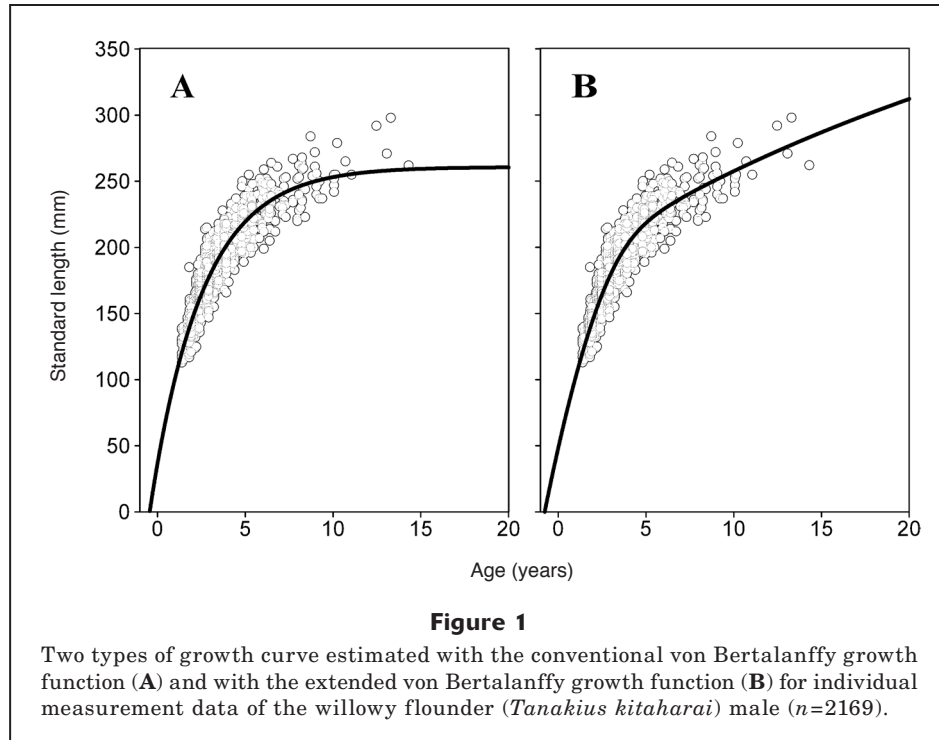
Results

Results for curve fitting and model selection are summarized in Table 1 and Figure 1. As shown in Table 1, the AIC difference (ΔAIC=20.8) between the two types of VBGF suggests that the trajectory given by the extended model more appropriately described lifetime growth. This result implies that a consideration of reproductive energy can be meaningful for model extensions. The variance of two common parameters (i.e., l_∞ and t_0) in the extended model was larger than that in the conventional VBGF (Table 1).

Twelve types of energy allocation schedules, $p(t)$, and the corresponding somatic growth (in length l) based on different combinations of parameter values in Equation 8 (v=0.4, 0.6, 0.8, 1.0 and a=1, 3, 100) are shown in Figure 2. The behavior of df/dt and f describing the energy investment in reproduction is shown in Figure 3.

When v=0, the growth curve is identical to the original VBGF (Fig. 2). Although somatic growth curves generated by lower v values (i.e., v=0.4, Fig. 2, A–C) do not differ substantially from the original VBGF, there are distinctive differences for shapes with higher v values (i.e., v=0.8, 1.0, Fig. 2, G–L). In these cases, the somatic growth of the adult and juvenile stages can be clearly distinguished. Gradual but steady growth after maturation is typical with indeterminate growth (Fig. 2, A–I). We can see a continuous phase shift of indeterminate growth in Figure 2. When v=1.0, the growth rate after maturation converges to zero because most surplus energy is devoted to reproduction, generating more determinate growth (Fig. 2, J–L).

The variation in a leads to a difference in the degree of continuity of growth rate during the sexual maturation transition period (Fig. 2, A, D, G, and J vs. Fig. 2, C, F, I, and L). The curves given by sufficiently high a (a=100) represent biphasic VBGF resulting from an abrupt change in growth rate around age t_m (Fig. 2, C, F, I, and L).

In Figure 3, an apex can be found on the convex shape of df/dt, and the height and degree of curvature changes according to the values of v and a. An increase in the value of v raises the reproductive investment $df/$

Figure 1

Two types of growth curve estimated with the conventional von Bertalanffy growth function (**A**) and with the extended von Bertalanffy growth function (**B**) for individual measurement data of the willowy flounder (*Tanakius kitaharai*) male (*n*=2169).

dt and shifts the maximum *df/dt* to older ages. When *v*=1.0 (Fig. 3, J–L), *df/dt* converges to a constant value after maturation as a result of determinate growth and constant surplus energy, defined by Equation 2. Lower *a* values show a slower initial rise in *df/dt* around t_m (Fig. 3, A, D, G, and J), whereas higher *a* values yield a steeper initial rise in *df/dt* around t_m (Fig. 3, C, F, I, and L).

Discussion

A notable feature of our model is that energy allocation can be quantified by the arbitrary functional form *p*(·). The introduction of *p*(·) provides a unified platform to treat the trade-off between somatic growth and reproduction. The extended model can jointly describe adult and juvenile growth. The change in growth rate between the two stages can be either gradual or steep, with the latter case showing a biphasic VBGF. By controlling the value of *p*(·), our comprehensive model yields various shapes of growth curves that range from indeterminate to determinate growth. Therefore, our model can be used for life history studies, as well as practical curve fitting studies. When allocation dynamics are not fully described by a simple model, such as seen in Equation 8, additional parameters beyond *a*, *v*, and t_m, or a particularly designed form of *p*(·) would be useful for further model development.

The extended VBGF in Equation 5 can theoretically incorporate an unlimited number of parameters. However, an increase in the number of free parameters in *p*(·) will be disadvantageous for model estimation because the functional form of *p*(·) does not directly appear in the age-length relationship. Increases in the variance of estimates imply instability due to curve fitting (Table 1). Therefore, it is necessary to consider methods of overcoming the trade-off between an increased number of parameters and estimation stability. Data sets other than those for length-at-age data will be useful for estimating the parameters in *p*(·) because the dynamics of *p*(·) are readily apparent in the behavior of *df/dt* (Fig. 3) rather than in length (Fig. 2). We expect that the robustness of this estimation will be improved by means of a combined likelihood-function (Martin and Cook, 1990; Eveson et al., 2004) described by two heterogeneous relationships: length-at-age and reproductive energy-at-age.

Our model development has similarities to that of Lester et al. (2004). Both studies explicitly give a growth function that can quantify a delay in somatic growth due to reproductive energy allocation. Lester et al. (2004) initially assumed a linear function of premature growth in length and derived the conventional VBGF by introducing an intensive energy investment at postmature ages. Additionally, Lester et al. (2004) assumed that the ratio of gonad to body weight at postmature ages is constant. This assumption causes the linear function to yield a delay in growth after maturation equivalent to that yielded with the VBGF. Alternatively, our model derivation started from the VBGF. Additional hypotheses for model formulation other than ours and those of Lester et al. (2004) are possible. Hence, the adequacy of these assumptions for model derivation must be evaluated with a wide range of practical applications.
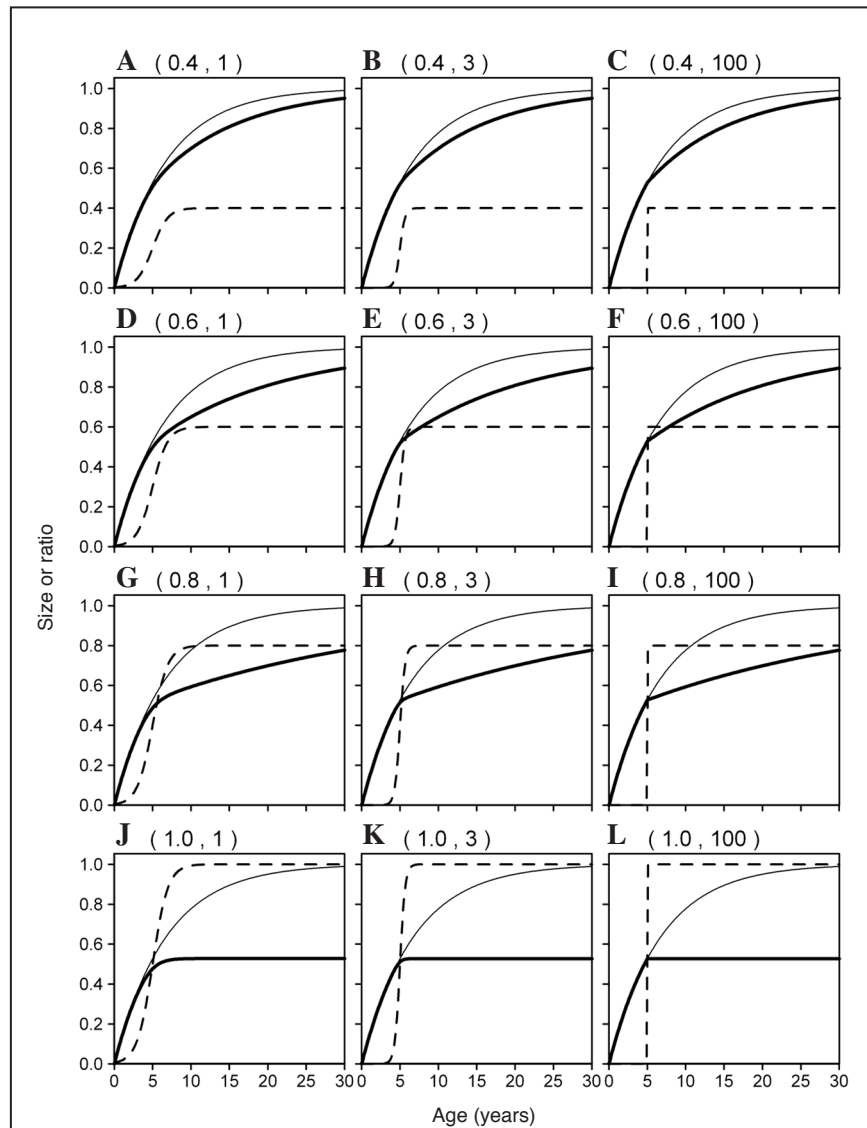
Figure 2

Variation in somatic growth due to differences in energy allocation (**A–L**). Thick, thin, and broken lines correspond to growth in length $l(t)$, growth in length $l(t)$ with $v=0$ (i.e., the original von Bertalanffy growth function), and the energy allocation function $p(t)$, respectively. The numerical values in parentheses correspond to the combination of parameters $v(=0.4, 0.6, 0.8, 1.0)$ and $a(=1, 3, 100)$ employed in $p(t)$. The parameters used for all cases include the following: $\beta=1.0$, $c=1.0$, $K=0.15$, $l_\infty=1.0$, $t_0=0$, and $t_m=5$.

Acknowledgments

Figure 3

Variation in variables related to reproduction that result from differences in energy allocation (**A–L**). Thick, thin, and broken lines correspond to the instantaneous reproductive energy df/dt, cumulative energy investment $f(t)$, and the energy allocation function $p(t)$, respectively. The numerical values in parentheses correspond to the combination of parameters $v(=0.4, 0.6, 0.8, 1.0)$ and $a(=1, 3, 100)$ employed in $p(t)$. The parameters used for all cases include the following: $\beta=1.0$, $c=1.0$, $K=0.15$, $l_\infty=1.0$, $t_0=0$, and $t_m=5$.
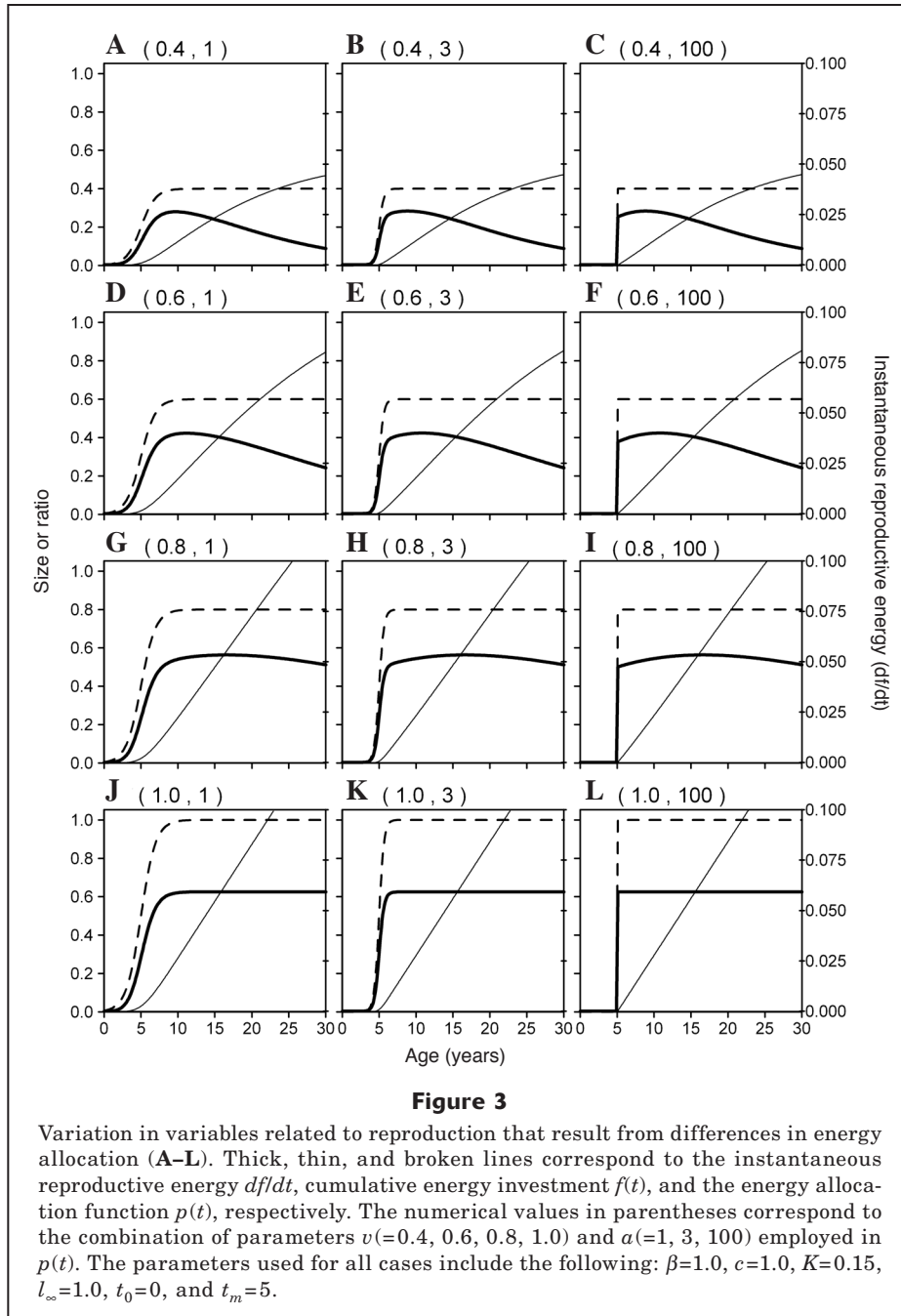
Literature cited

Akaike, H.
    1973. Information theory and an extension of the maximum likelihood principle. *In* 2nd international symposium on information theory (B. N. Petrov, and F. Csaki, eds.), p. 267–281. Akademiai Kiado, Budapest.

Alós, J., M. Palmer, A. Alonso-Fernández, and B. Morales-Nin.
    2010. Individual variability and sex-related differences in the growth of *Diplodus annularis* (Linnaeus, 1758). Fish. Res. 101:60–69.

Araya, M., and L. A. Cubillos.
    2006. Evidence of two-phase growth in elasmobranchs. Environ. Biol. Fish. 77: 293–300.

Beverton, R. J. H.
    1992. Patterns of reproductive strategy parameters in some marine teleost fishes. J. Fish Biol. 41:137–160.

Czarnołęski, M., and J. Kozłowski.
    1998. Do Bertalanffy's growth curves result from optimal resource allocation ? Ecol. Lett. 1:5–7.

Day, T., and P. D. Taylor.
    1997. Von Bertalanffy's growth equation should not

be used to model age and size at maturity. Am. Nat. 149:381–393.

Eveson, J. P., G. M. Laslett, and T. Polacheck.
2004. An integrated model for growth incorporating tag-recapture, length-frequency, and direct aging data. Can. J. Fish. Aquat. Sci. 61:292–306.

Jensen, A. L.
1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can. J. Fish. Aquat. Sci. 53:820–822.

Jørgensen, C., and Ø. Fiksen.
2006. State-dependent energy allocation in cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 63:186–199.

Kozłowski, J.
1992. Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. Trends Ecol. Evol. 7:15–19.
1996. Optimal allocation of resources explains interspecific life-history patterns in animals with indeterminate growth. Proc. R. Soc. Lond. B 263:559–566.

Kozłowski, J., and A. T. Teriokhin.
1999. Allocation of energy between growth and reproduction: The Pontryagin Maximum Principle solution for the case of age- and season-dependent mortality. Evol. Ecol. Res. 1:423–441.

Lester, N. P., B. J. Shuter, and P. A. Abrams.
2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. Proc. R. Soc. Lond. B 271:1625–1631.

Lincoln, R. J., G. A. Boxshall, and P. F. Clark.
1998. A dictionary of ecology, evolution and systematics, 361 p. Cambridge Univ. Press, New York.

Martin, I., and R. M. Cook.
1990. Combined analysis of length and age-at-length data. J. Cons. Int. Explor. Mer 46:178–186.

Ohnishi, S., and T. Akamine.
2006. Extension of von Bertalanffy growth model incorporating growth patterns of soft and hard tissues in bivalve molluscs. Fish. Sci. 72:787–795.

Pecquerie, L., P. Petitgas, and S. A. L. M. Kooijman.
2009. Modeling fish growth and reproduction in the context of the Dynamic Energy Budget theory to predict environmental impact on anchovy spawning duration. J. Sea Res. 62:93–105.

Porch, C. E., C. A. Wilson, and D. L. Nieland.
2002. A new growth model for red drum (*Sciaenops ocellatus*) that accommodates seasonal and ontogenic changes in growth rates. Fish. Bull. 100:149–152.

Quince, C., P. A. Abrams, B. J. Shuter, and N. P. Lester.
2008a. Biphasic growth in fish I: theoretical foundations. J. Theor. Biol. 254:197–206.

Quince, C., B. J. Shuter, P. A. Abrams, and N. P. Lester.
2008b. Biphasic growth in fish II: empirical assessment. J. Theor. Biol. 254:207–214.

Quinn, T. J., II, and R. B. Deriso.
1999. Quantitative fish dynamics, 542 p. Oxford Univ. Press, New York.

R Development Core Team.
2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from: URL http://www.R-project.org]

Roff, D. A.
1983. An allocation model of growth and reproduction in fish. Can. J. Fish. Aquat. Sci. 40:1395–1404.
1984. The evolution of life history parameters in teleosts. Can. J. Fish. Aquat. Sci. 41:989–1000.

Schnute, J. T., and L. J. Richards.
1990. A unified approach to the analysis of fish growth, maturity, and survivorship data. Can. J. Fish. Aquat. Sci. 47:24–40.

Soriano, M., J. Moreau, J. M. Hoenig, and D. Pauly.
1992. New functions for the analysis of two-phase growth of juvenile and adult fishes, with application to Nile perch. Trans. Am. Fish. Soc. 121:486–493.

Tribuzio, C. A., G. H. Kruse, and J. T. Fujioka.
2010. Age and growth of spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska: analysis of alternative growth models. Fish. Bull. 108:119–135.