PERSPECTIVE

A stage-explicit expression of the von Bertalanffy growth model for understanding age at first reproduction of Great Lakes fishes

Ji X. He and Donald J. Stewart

Abstract: An initial annual growth rate of body length and its regular decrease with increasing age has general linkages with age at first reproduction (t_R) . We clarify their combinations and develop predictive functions. We use a complete Ford–Walford plot with yearling size (L_1) on the *y* axis and show a slope transition between the relative yearling growth rate (ρ_y) and the Ford–Walford slope (ρ) . The three stage-specific variables define a complete body-length trajectory over ages, including all von Bertalanffy growth parameters and the Ford–Walford intercept (L_{int}) . The difference between asymptotic length (L_{inf}) and yearling length is growth potential after the first annulus. Yearling growth is a transition period, so growth potential can be adjusted as ρL_{inf} or $L_{inf} - L_{int}$. Changes in the three life-stage variables have contrasting effects on growth potential and von Bertalanffy growth parameters, so they have contrasting relations with t_R . For most invertebrate-eating fishes in the Laurentian Great Lakes, dominant changes in growth trajectories were reflected in ρ , so t_R was predicted by the von Bertalanffy growth coefficient, *K*. For walleye (*Stizostedion vitreum*) populations around the Great Lakes, dominant changes in growth trajectories were from yearling size or yearling growth, so t_R was predicted using L_{int} . Our results have clear implications for understanding fish population dynamics.

Résumé : Le taux initial de croissance annuelle en taille et sa décroissance graduelle avec l'âge sont en relation générale avec l'âge à la première reproduction ($t_{\rm R}$). Nous mettons en lumière les différentes combinaisons de ces liens et développons des fonctions prédictives. Nous utilisons un graphique complet de Ford-Walford avec la taille des poissons de 1 an (L_1) en ordonnée et démontrons l'existence d'une transition de pente entre le taux relatif de croissance des poissons de 1 an (ρ_v) et la pente de Ford-Walford (ρ). Les trois variables spécifiques au stade définissent la trajectoire complète de la taille au cours de la vie, y compris les paramètres de croissance de Bertalanffy et le point de croisement de Ford-Walford (L_{int}). La différence entre la longueur asymptotique (L_{inf}) et la longueur des poissons de 1 an représente le potentiel de croissance après le premier anneau de croissance. Comme la croissance des poissons de 1 an représente une période de transition, le potentiel de croissance peut donc être ajusté en fonction de (pL_{inf}) ou de (L_{inf}) $L_{\rm int}$). Les variations des trois variables du cycle biologique ont des effets différents sur le potentiel de croissance et les paramètres de von Bertalanffy, et, par conséquent, sur $t_{\rm R}$. Chez la plupart des poissons des Grands-Lacs qui se nourrissent d'invertébrés, les changements principaux dans les trajectoires de croissance se reflètent dans les pentes de Ford-Walford et ainsi $t_{\rm R}$ peut être prédit à partir de K. Chez les populations de dorés (Stizostedion vitreum) de la région des Grands-Lacs, les changements importants dans les trajectoires de croissance sont reliés à la taille ou à la croissance des poissons de 1 an et t_R peut alors être prédit d'après L_{int} . Nos résultats sont importants pour la compréhension de la dynamique des populations de poissons.

[Traduit par la Rédaction]

Received 10 September 2001. Accepted 24 January 2002. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 22 February 2002. J16522

J.X. He^{1,2} and D.J. Stewart. State University of New York, College of Environmental Science and Forestry, 103 Illick Hall, 1 Forestry Drive, Syracuse, NY 13210, U.S.A.

¹Corresponding author (e-mail: jhe@zoo.utoronto.ca).

²Present address: Department of Zoology, 25 Harbord Street, University of Toronto, Toronto, ON M5S 3G5, Canada.

Introduction

Relations between body growth and age at first reproduction need to be further clarified, and the goal is to find quantitative predictive relations. Rapid growth in young ages can lead to early age at first reproduction (e.g., Alm 1959), whereas a slow decrease in annual growth with increasing age may lead to late age at first reproduction (e.g., Martin 1970; Matuszek et al. 1990). Recent studies have addressed combinations of the above two different relations (Hutchings 1993; Jonsson and Jonsson 1993; Fox 1994), but reaction norms summarized by Stearns (1992) did not sufficiently address those complexities (see also Berrigan and Charnov 1994).

There have been many studies that relate age or size at first reproduction to von Bertalanffy growth parameters (Beverton 1992; Charnov 1993; Jensen 1996). Those empirical relations are general patterns, and very often, their emphasis is not accuracy of predictions. A promising approach to understanding age or size at first reproduction is to include more independent variables like mortality (e.g., Roff 1984), but in broad practical applications, body growth is often the only reliable information. In a previous study for 85 marine and freshwater fish species with 235 observations, most of the variance in size and age at first reproduction was explained by body growth alone (He and Stewart 2001). A similar perspective was presented by Shuter et al. (1998). It is still a challenge to build on general patterns and demonstrate accurate prediction of changes in age or size at first reproduction.

We propose that the theoretical basis for practical prediction may have to involve consideration for stage-specific effects of body growth. Along that line, typical life-stage compositions of normal growth trajectories must be demonstrated, although those trajectories have been commonly described as continuous processes. In this paper, we have two sets of objectives. (*i*) To develop a stage-explicit expression of the commonly used von Bertalanffy growth model (VBGM, von Bertalanffy 1938) and to clarify the concept of growth potential that has been used implicitly to study age and size at first reproduction; (*ii*) to apply the stage-explicit model to analyze fishes in the Laurentian Great Lakes, and thereby, to develop accurate predictive relations between body growth and age at first reproduction.

State-explicit expression of VBGM and the concept of growth potential

The commonly used expression of the von Bertalanffy growth model emphasizes continuity of a growth process. With that emphasis alone, there have been difficulties for studying relations between body growth and age at first reproduction.

(1)
$$dL/dt = K(L_{inf} - L)$$

(2)
$$L_t = L_{inf} [1 - \exp(-K(t - t_0))]$$

Here, *L* is body length at a given age (*t*), *K* is the von Bertalanffy growth coefficient, and L_{inf} is asymptotic body length. There are three well-known ambiguous concepts in the model expression: (*i*) the maximum growth rate (*E* =

 KL_{inf}) is hypothetical because it corresponds to zero body length; (*ii*) the coefficient K accounts for both rapid growth and rapid decreases in annual growth; (*iii*) the age with zero body length (t_0) is defined mathematically, and nonzero values for t_0 have not been explained biologically. Assuming t_0 is always negative, a body length at age 0 could be body length at birth or at hatching (Pauly 1981; Charnov 1993). With complete data from age 1 to much older, however, there is no reason to exclude t_0 values that are positive and less than 1.

We can express the same growth process as a combination of stage-specific components:

(3)
$$L_2 = L_1 + \rho_v L_1$$

(4)
$$L_{t+1} - L_t = \rho(L_t - L_{t-1})$$
 $t \ge 2, \ 0 < \rho < 1$
or $L_t = L_{int} + \rho L_{t-1}$ $t \ge 2, \ 0 < \rho < 1$

where L_1 is body length at age 1, ρ_y is the relative growth rate of a yearling, ρ is the Ford–Walford slope, and L_{int} is the Ford–Walford intercept (Ford 1933; Walford 1946; Ricker 1975).

Combining eqs. 3 and 4, we have an elementary geometrical progression:

(5)
$$L_t = L_1 + \rho_y L_1 \Sigma \rho^i$$
 $i = 0, 1, 2, ..., t - 1$
or $L_t = L_1 + \rho_y L_1 (1 - \rho^{t-1})/(1 - \rho)$

With eqs. 3–5, the following biological details are clear. (*i*) When t = 1, the whole model is reduced to yearling size, indicating that L_1 is an input variable and is not influenced by the relations that control the subsequent growth process. (*ii*) When t = 2, eq. 5 is identical to eq. 3, indicating that the geometric growth of a yearling represents a special transition period. (*iii*) After age 2, annual growth of body length decreases regularly, and ρ is the proportion of annual growth that can be maintained at every age interval (eq. 4).

A critical point of eqs. 1–5 is about biological meanings of L_{int} and the parameter t_0 . Those biological meanings were not clear because they have not been defined using measurable variables (see Ford 1933; Walford 1946; Ricker 1975). To clarify conceptual ambiguities, we use a complete Ford-Walford plot that has yearling size on the y axis (Fig. 1*a*). The line from $(0, L_1)$ to (L_1, L_2) has a slope of ρ_y that represents the relative growth rate of a yearling (eq. 3). ρ is for the line starting from (L_1, L_2) , and the slope is no longer a growth rate (eq. 4). Quantitatively, ρ_y and ρ often represent a slope transition. L_{int} may differ from yearling size (L_1) simply because of the slope transition (Fig. 1*a*)

(6)
$$L_{\text{int}} = L_1(1 + \rho_y - \rho)$$

Correspondingly, the slope transition also leads to a nonzero parameter, t_0 , in eq. 2

(7)
$$t_0 = 1 - \ln[\rho_v/(1 + \rho_v - \rho)]/\ln(\rho)$$

If $\rho_y < \rho$, then $L_{int} < L_1$, and t_0 is negative. If $\rho_y > \rho$, then $L_{int} > L_1$ and t_0 is positive. In the latter case with a complete data set including yearling size, t_0 should always be less than 1 because yearling size cannot be zero or negative. In a special case where the two slopes of ρ_y and ρ are quantitatively the same, $t_0 = 0$ and $L_{int} = L_1$.

Fig. 1. A new and complete interpretation of the von Bertalanffy growth model and its implication for predicting age at first reproduction (t_R). Details about data for (b-d) are in subsequent sections of the text. (*a*) The complete Ford–Walford plot for a hypothetical body-growth trajectory with von Bertalanffy growth parameters $L_{inf} = 90$ cm, K = 0.16, and $t_0 = -2$ (eq. 2). The difference between asymptotic length (L_{inf}) and yearling size (L_1) is growth potential (GP) because L_1 is an input variable on the y axis. The slope (ρ_y) is the relative growth rate of yearlings (eq. 3), and the Ford–Walford slope (ρ) after age 2 is not a growth rate (eq. 4). Because yearling growth represented by ρ_y is a transition period, growth potential can be adjusted as ρL_{inf} or $L_{inf} - L_{int}$, where L_{int} is the Ford–Walford intercept (eq. 6). The three stage-specific variables (L_1 , ρ_y , ρ) are actually elements that define the growth trajectory (eqs. 5–9). (*b*) Applying eq. 5 to fit growth data, estimated L_1 as a growth parameter is not statistically different from observed yearling size (L_1). (*c*) The parameter t_0 represents the direction and magnitude of slope transition between ρ_y and ρ ; the exact relation is eq. 7. (*d*) Two major different tracks for the relation between t_R and the growth coefficient (*K*). One is for eight walleye populations, and the other is for 23 populations of invertebrate-eating fishes. Those two sets of distinguishable cases may differ in relative dominance of the three major life stages (*a*); details are analyzed in Results.



Mathematically, eq. 5 is the simplest form of two general expressions of the von Bertalanffy growth model (Knight 1969; Schnute and Fournier 1980). Other parameters of eqs. 1–2 can be defined also by stage-specific variables in eq. 5

(8)
$$K = -\ln(\rho)$$

(9)
$$L_{inf} = L_1(1 + \rho_v - \rho)/(1 - \rho)$$

Derivations of eqs. 6–9 are not represented here because they can be obtained by using L_1 , ρ_y , and ρ with equations in Knight (1969) and Schnute and Fournier (1980). It is not arbitrary to use the three stage-specific variables (L_1 , ρ_y , ρ) because they are elements of a complete growth trajectory and they cannot be further decomposed. They allow us to recognize that the complete Ford–Walford plot (Fig. 1*a*) is an exact expression of the von Bertalanffy growth model (eqs. 1–5). To use the von Bertalanffy growth model, we do not rely on hypothetical concepts such as nonzero body length at age 0 or maximum growth rate with a body length of zero.

With the above stage-explicit expression of the von Bertalanffy growth model, we can specify the concept of growth potential. Rearranging eq. 9, we have

(10)
$$(\rho_v L_1)/(1-\rho) = L_{inf} - L_1$$

On the left side, the numerator $(\rho_y L_1)$ is the maximum annual growth after the first year of a life, and the denominator $(1 - \rho)$ is the proportional decay in annual growth after age 2. On the right side, L_1 is an input variable (eq. 5), and L_{inf} is

asymptotic body length. Both sides express growth potential after age 1, and the concept is consistent with eqs. 3–5.

There are two possible ways by which the growth potential may increase or decrease. In the first, with a given set of values for L_1 and ρ_y , the growth potential can be increased by increasing ρ and L_{inf} (Fig. 1*a*). In the second, with a given L_{inf} , the growth potential can be decreased by increasing yearling size (L_1). For the latter case, there may be a negative relation between ($\rho_y L_1$) and ρ , but we must notice that ($\rho_y L_1$) represents a transition period with two components (eqs. 3 and 5; Fig. 1*a*). One component is L_1 and the other component is ρ_y . Increases in ρ_y with a given L_1 may increase the growth potential by increasing asymptotic size, or it may influence ρ without having any impact on the growth potential (eq. 10). The concept of growth potential may need to be adjusted because of the two possibilities of ρ_y effects.

There are a number of ways to adjust the concept of growth potential. From eqs. 6 and 9, we have the commonly used relation between the Ford–Walford intercept and asymptotic size

(11)
$$L_{\text{int}}/(1-\rho) = L_1 (1+\rho_v - \rho)/(1-\rho) = L_{\text{inf}}$$

Equation 11 suggests that improvement of body growth at each of the three life stages, represented by L_1 , ρ_y , and ρ , can always increase L_{inf} . Such a suggestion is consistent with the model expression of eqs. 1–2, where L_{inf} is regarded as the lifetime growth potential staring from zero body length. Alternatively, we consider that each stage may occupy different environments, and growth in each stage is often controlled by different relations (eqs. 3–5). Rearranging eq. 11, we have

(12)
$$(\rho L_{inf}) = (L_{inf} - L_{int})$$

In comparison with eq. 10, L_1 is replaced by L_{int} . The emphasis here is that $\rho_y L_1$ and L_1 jointly represent an early life stage (Fig. 1*a*), whereas ρL_{inf} or $L_{inf} - L_{int}$ are an alternative index of growth potential for subsequent juvenile–adult growth. With a given L_{inf} , an increase in either L_1 or ρ_y can decrease the adjusted growth potential by increasing the intercept (L_{int} , eq. 6; Fig. 1*a*).

It may be worthwhile to mention a qualitative difference between body-length and body-mass growths, because eq. 12 treats adult growth and a major part of juvenile growth as a single stage. Annual growth of somatic body mass increases with age before the first reproduction, and it decreases with increasing age after first reproduction (e.g., Jensen 1985). An emphasis on that stagnation of body-mass growth, however, may not allow us to explore the effects of multiple life stages that significantly influence age at first reproduction long before that age is reached. At the age of first reproduction, an acceleration of decreases in bodylength growth has also been suggested (Stamps et al. 1998), but many empirical syntheses have not shown such an acceleration (e.g., Iles 1974; Ricker 1975; Moreau 1987). If age at first reproduction is larger than 2, the annual proportional decrease $(1 - \rho)$ in body-length growth is typically the same for both premature and postmature periods. If there is an acceleration of decreases in annual body-length growth corresponding to first reproduction, the commonly used von Bertalanffy growth model would always overestimate body length for mature age classes whenever age at first reproduction is larger than 2.

Growth potential and age at first reproduction

A change in growth potential (eq. 12) should be a basis for predicting changes in age at first reproduction. Such a basis can be justified using functional linkages between body length and age at first reproduction. There is a general pattern as follows (He and Stewart 2001):

(13)
$$L_{\rm R}/(KL_{\rm inf}) = a + bt_{\rm R}$$

where $L_{\rm R}$ and $t_{\rm R}$ are body length and age at first reproduction, a and b are regression parameters, and b is always positive. An alternative expression of the left side is $[1 - \exp(-K)]$ $(t_{\rm R} - t_0))]/K$. The two expressions include either $L_{\rm R}$ or $t_{\rm R}$ with a given set of growth parameters. Those growth parameters define a functional linkage between $L_{\rm R}$ and $t_{\rm R}$ for a given growth trajectory, so we can call the left side an index for growth-reproduction linkage (I_{G-R}) . On the right side of eq. 13, the structure with regression parameters is representative of many growth trajectories, so it is not a linear simplification of the left-side structure. There are two interrelated ideas here. (i) When the two sides of eq. 13 are equal as demonstrated by empirical data, there must be a fundamental linkage between body length and age at first reproduction regardless of substantial changes in body-growth trajectories. (ii) Such a linkage indicates a potential relation between growth potential and age at first reproduction. Because $K = -\ln(\rho)$ (eq. 8), the negative relation between KL_{inf} and $t_{\rm R}$ suggests that $t_{\rm R}$ should be positively related to growth potential (ρL_{inf} , eq. 12).

In practical applications, a statistical difficulty may stem from different life stages having contrasting effects on growth potential. When dominant changes are from L_{inf} and ρ , slow decreases in annual growth after age 2 are related to increases in growth potential (eqs. 10 and 12). When dominant changes are from L_1 and ρ_y , large sizes at a given age (particularly a young age) are associated with decreases in growth potential (eq. 12). It is almost impossible to separate those contrasting stage-specific effects.

To overcome the above difficulty, we need case-specific analyses. If dominant changes in body growth are represented by the positive relation between ρ and L_{inf} , or the negative relation between K and L_{inf} , the only dominant predictive variable in eq. 13 will be K. If dominant changes in body growth are represented by L_1 and ρ_v , there will be no significant relation between ρ and L_{inf} , or between K and L_{inf} , but there is always a negative relation between ρ and $L_{\rm int}$ (eq. 6). Comparing the above two typical cases, parameter values for the right side of eq. 13 should be notably different. If we can separate typical cases according to statistical features for life-stage combinations, it may become possible to find an accurate predictive relation between $t_{\rm R}$ and ρ , or between $t_{\rm R}$ and $L_{\rm int}$. The two potential predictive relations are not necessarily interchangeable, although L_{int} and ρ are related to each other for a given growth trajectory (eq. 11). Among various growth trajectories, changes in L_{int} and ρ may have different relative dominances because body-growth trajectories can be influenced mostly by one or two of the three major life stages, represented by L_1 , ρ_y , and ρ .

When we use ρ or L_{int} as an independent variable for predicting changes in age at first reproduction, such a predictive parameter integrates dominant and subordinate factors of growth potential; meanwhile, they also allow for an emphasis on the dominant factor (see eq. 12). If dominant changes are from L_{inf} , the slope ρ will emphasize its positive relation with L_{inf} , while it also integrates potential impacts from the intercept (L_{int}). To demonstrate the point, we can rearrange eqs. 13 and 9, and have

(14)
$$\rho = 1 - (L_{int}/L_{inf})$$

(15)
$$\rho = [L_{int} - L_1(1 + \rho_y)]/(L_{inf} - L_1)$$

If dominant changes are from L_1 and ρ_y , L_{int} should be used to emphasize changes in those two dominant variables, whereas L_{int} will also integrate subordinate impacts of asymptotic size on ρ (eqs. 6 and 14).

Empirical data, life-history variables, and growth parameters

Our data cover major fish species in the Laurentian Great Lakes, including alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), lake whitefish (*Coregonus clupeaformis*), round whitefish (*Prosopium cylindraceum*), pygmy whitefish (*Prosopium coulteri*), lake herring (*Coregonus artedii*), kiyi (*Coregonus kiyi*), bloater (*Coregonus hoyi*), gizzard shad (*Dorosoma cepedianum*), yellow perch (*Perca flavescens*), white perch (*Morone americana*), and walleye (*Stizostedion vitreum*).

Most of those species are primarily invertebrate-eating fishes. For those species, we restrict data to populations within the Laurentian Great Lakes because combinations of stage-explicit growth may have different quantitative features in other ecosystems. Walleye is a piscivore, and on a yearly scale, its primary diet typically switches from invertebrates to fish during yearling growth. We included walleye populations from other lakes where prey fishes are major food resources to the predator. Lake trout (Salvelinus namaycush) is also a very important species in the Great Lakes, but we have provided analysis elsewhere (He and Stewart 2001). Here, it is sufficient to mention that the relation between body growth and age at first reproduction is similar between walleye and lake trout around the Great Lakes. Sculpins also form an important group of benthic fishes in the Laurentian Great Lakes, but published data are not sufficient for a synthetical analysis in the present context.

Data on size at age and age at first reproduction were collected from published studies on size at age and on age at first reproduction (Appendix A). Information for growth and age at first reproduction was for the same fish population (i.e., from the same area and period). Most of the species have been analyzed independently several times based on hundreds or thousands of samples. Because size at age was from back calculation with large samples, biases were minimized. We only analyzed data for females, although our general methods are applicable to both males and females (He and Stewart 2001). When sex was not identifiable in a young age, growth of males and females was normally the same as was detailed in those empirical studies.

Size at age is the total body length corresponding to an annulus and age 1 is always treated as the age at the first annulus. Age at first reproduction is the number of annuli at first reproduction. If an age-2+ fish has reached sexual maturity and has spawned in the spring or early summer of its third year of life, its age at first reproduction is age 2. If an age-2+ fish has reached sexual maturity but has spawned in the fall or winter of its third year of life, its age at first reproduction is age 3. Such a definition of age at first reproduction reflects the completion of growth seasons and allows for comparisons between spring spawners and fall spawners. We used mean age at first reproduction, or the first age when 50% or more of females attain sexual maturity.

Growth parameters with eqs. 5 and 2 were estimated using nonlinear regression for each fish population (SAS NLIN procedure, SAS Institute Inc. 1999). For three populations of walleye, von Bertalanffy growth parameters are from the original study by Craig et al. (1995).

Results of data analyses

Stage-specific variables and von Bertalanffy growth parameters

Stage-specific variables with eq. 5 and all conventional von Bertalanffy growth parameters with eq. 2 are summarized in Table 1. Except for three walleye populations mentioned in the above section, those variables and parameters were estimated separately with different equations, but estimates for each population are exactly interchangeable using eqs. 6-9. There is no significant difference between estimated and observed yearling sizes (Fig. 1b). A plot of estimated parameter t_0 versus the ratio of ρ_v to ρ provides a clear demonstration of the functional relation of eq. 7 (Fig. 1c). With limited space, we cannot present all of the statistical details for 28 populations. The essential information represented in Table 1 and Appendix A, however, should be sufficient for residual analysis and for evaluating statistical quality. Our conclusion is that eqs. 5 and 2 properly and even accurately provided the same expression for each bodygrowth trajectory.

Differences between walleye and invertebrate-eating fishes

For both walleye and invertebrate-eating fishes studied here, L_{int} has a positive correlation with body size at age 2 (L_2) and a negative correlation with ρ (Table 2). Those correlations are consistent with eq. 6. A plot of $\log_{10}(t_R)$ versus $\log_{10}(K)$, however, indicates potential differences between populations of walleye and invertebrate-eating fishes. With a similar range of t_R , there is a much wider range of K values for invertebrate-eating fishes than for walleye (Fig. 1*d*).

For those walleye populations, L_{inf} has positive correlations with both L_2 and L_{int} , but no relation with ρ (Table 2). In such a case, the negative correlation between ρ and L_{int} can be explained as follows. When L_{int} , L_2 , and L_{inf} increase, proportional increases in L_{int} and L_2 must be larger than proportional increases in L_{inf} , so ρ can decrease with increasing L_{int} (Fig. 1*a*). The first two years of body growth apparently have the dominant effect that leads to changes in ρ . Varia-

Table 1. Conventional von Bertalanffy growth parameters (L_{inf} , K, t_0) using eq. 2, stage-specific growth parameters (L_1 , ρ_y , ρ , L_{int}) using eqs. 5–6, and age at first reproduction (t_R) for 31 fish populations.

Reference	Species	$L_{ m inf}$	Κ	t_0	L_1	ρ_{y}	ρ	$L_{\rm int}$	t _R
Van Osten and Hile 1949	Lake whitefish	609	0.345	-0.058	186	0.662	0.708	178	4.0
Van Osten 1939	Lake whitefish	732	0.224	0.258	112	1.111	0.800	147	5.0
Mraz 1964 <i>a</i>	Lake whitefish	654	0.332	0.114	167	0.827	0.718	185	4.0
Dryer 1963	Lake whitefish	771	0.126	-0.470	130	0.582	0.882	91	7.0
Edsall 1960	Lake whitefish	609	0.063	-3.485	151	0.187	0.939	37	12.0
Bailey 1963	Round whitefish	460	0.201	-0.481	118	0.525	0.818	84	5.0
Mraz 1964 <i>b</i>	Round whitefish	561	0.268	0.091	121	0.853	0.765	132	4.0
Armstrong et al. 1977	Round whitefish	518	0.382	0.189	138	0.874	0.682	165	3.0
Eschmeyer and Bailey 1954	Pygmy whitefish	151	0.275	-0.289	45	0.565	0.760	36	4.0
Dryer and Beil 1964	Lake herring	391	0.298	-0.216	119	0.591	0.743	101	4.0
Dryer and Beil 1968	Bloater	329	0.196	-0.956	105	0.381	0.822	59	3.0
Deason and Hile 1947	Kiyi	285	0.434	-0.285	122	0.472	0.648	100	2.0
Brown 1972	Alewife	196	0.581	-0.187	98	0.444	0.559	87	3.0
Bronte et al. 1991	Alewife	191	1.053	0.402	89	0.742	0.349	124	2.0
O'Gorman et al. 1997	Alewife	170	0.752	0.013	89	0.480	0.471	90	2.5
Norden 1967	Alewife	183	0.692	-0.039	94	0.474	0.501	91	2.0
Bailey 1964	Rainbow smelt	270	0.488	0.412	67	1.162	0.614	104	3.0
Bodola 1965	Gizzard shad	395	0.775	0.428	142	0.968	0.461	213	2.0
Jobes 1952	Yellow perch	300	0.439	0.134	95	0.768	0.645	107	3.0
El-Zarka 1959	Yellow perch	622	0.083	-0.372	67	0.660	0.920	50	4.0
Hile and Jobes 1942	Yellow perch	472	0.130	-0.243	70	0.696	0.878	57	4.0
Wells 1983	Yellow perch	355	0.358	0.228	86	0.946	0.699	107	3.0
Schaeffer and Margraf 1986	White perch	261	0.682	0.474	79	1.146	0.506	129	2.0
Wolfert 1969, 1977	Walleye	834	0.207	-0.594	234	0.478	0.813	156	3.0
Hile 1954	Walleye	721	0.284	0.082	166	0.830	0.753	178	3.0
Priegel 1969	Walleye	616	0.245	-0.174	154	0.652	0.782	134	6.0
Eschmeyer 1950	Walleye	571	0.266	0.037	129	0.801	0.767	133	5.0
Smith and Pycha 1961	Walleye	543	0.178	-0.744	145	0.448	0.837	88	8.0
Craig et al. 1995	Walleye	622	0.253	-0.193	162	0.634	0.776	139	5.0
Craig et al. 1995	Walleye	544	0.292	-0.682	211	0.399	0.747	138	5.0
Craig et al. 1995	Walleye	466	0.215	-0.632	138	0.460	0.807	90	7.0

Note: Corresponding growth data are in Appendix A. Relations between the two sets of growth parameters are eqs. 7–9. See parameter definitions and estimation methods in text.

tions in t_0 are mostly due to variations in ρ_y (Table 2), although ρ is another component for determining t_0 values (eq. 7).

For those invertebrate-eating fishes, asymptotic size (L_{inf}) has positive correlations with both L_2 and ρ , but no relation with L_{int} (Table 2). In such a case, when L_2 and L_{inf} increase, proportional increases in L_{inf} must be larger than proportional increases in L_2 , so ρ can increase with L_{inf} (Fig. 1*a*). Apparently, dominant changes in ρ are related to changes in asymptotic size. Meanwhile, because there is no relation between L_{inf} and L_{int} , and because the negative correlation between L_{inf} and ρ is always there, a small L_1 , or ρ_y , and a large L_{inf} can both contribute to a large ρ or small K (or vice versa, Fig. 1*a*). It is not surprising that variations in t_0 are due to variations in both ρ_y and ρ (Table 2).

Predicting age at first reproduction using growth parameters

For all invertebrate-eating fishes studied here, we can use K to predict $t_{\rm R}$. With 11 species and 23 populations, R^2 is 0.72. Four data points are far outside the confidence limits and are apparent outliers (Fig. 2*a*). Excluding those outliers,

we increase R^2 to 0.95 (Fig. 2*b*). The two data points with the largest t_R values are also outside the confidence limits in Fig. 2*a*, but that is because of effects from the four outliers mentioned above. Excluding the two data points with the largest t_R and including the four outliers distorted the regression, R^2 was only 0.59. Excluding all of those six points yielded regression parameters that were not statistically different from those in Fig. 2*b*.

The above results embody two contrasting relations. Because of the negative relation between K and L_{inf} (Table 2), a relatively small K, large ρ , and late t_R are largely due to slow decreases in annual growth after age 2. Because there is no relation between L_{inf} and L_{int} (Table 2), some small K, large ρ , and late t_R are due to very poor yearling growth associated with sufficiently large L_{inf} . The contrasting effects of different life stages can be found in both inter- and intra-specific comparisons (Table 1).

Two of the four outliers are the only two deep-water species in our analyses, bloater and kiyi. The fact that those two coregonines stand apart as outliers may be an indication that they are somehow special, rather than an invalidation of the general relation. Both species often have complex cycling of

	$L_{\rm int}$	L_1	ρ _y	L_2	ρ	L_{inf}	Κ	t_0
Eight p	opulations of v	walleye						
$L_{\rm int}$	1.0000	0.4964	0.5563	0.8423	-0.6469	0.7765	0.6457	0.6031
		0.2109	0.1521	0.0087	0.0830	0.0234	0.0838	0.1135
L_1		1.0000	-0.4289	0.8794	-0.0961	0.6390	0.0995	-0.3733
			0.2890	0.0040	0.8210	0.0881	0.8147	0.3624
$\rho_{\rm v}$			1.0000	0.0476	-0.4975	0.2617	0.4923	0.9836
				<u>0.9109</u>	0.2097	<u>0.5312</u>	0.2153	< <u>0.0001</u>
L_2				1.0000	-0.3429	0.8596	0.3440	0.0987
					0.4056	0.0062	0.4041	0.8162
ρ					1.0000	-0.0309	-0.9999	-0.5888
						0.9421	< <u>0.0001</u>	0.1246
L_{inf}						1.0000	0.0291	0.2590
							0.9456	0.5357
K							1.0000	0.5822
								0.1300
t_0								1.0000
Twenty	-three populati	ions of invertel	brate-eating fishe	S				
L _{int}	1.0000	0.5907	0.5999	0.8635	-0.4411	0.2372	0.4005	0.5582
		0.0030	0.0025	< <u>0.0001</u>	<u>0.0351</u>	0.2759	<u>0.0582</u>	0.0056
L_1		1.0000	-0.1353	0.8884	0.1239	0.5770	-0.1387	-0.2368
			0.5382	< <u>0.0001</u>	0.5733	0.0039	0.5280	0.2766
$\rho_{\rm v}$			1.0000	0.3172	-0.2682	0.1113	0.2318	0.7088
				0.1402	0.2159	<u>0.6130</u>	0.2871	0.0002
L_2				1.0000	-0.0236	0.5902	-0.0089	0.1514
					0.9149	0.0030	0.9679	0.4905
ρ					1.0000	0.6856	-0.9902	-0.5643
						0.0003	<0.0001	0.0050
L_{inf}						1.0000	-0.6651	-0.2516
V							0.0005	0.2468
Λ							1.0000	0.0122
4								<u>0.0122</u> 1.0000
ı ₀								1.0000

Table 2. Correlation coefficients and their p values (below, underlined) among von Bertalanffy growth parameters (eq. 2) and stage-specific variables (eq. 5).

Note: Included also are the Ford–Walford intercept (L_{int}) and body length at age 2 (L_2). L_{int} is a combination of three stage-specific variables (eq. 6) and L_2 is a combination of two stage-specific variables (eq. 3).

life-history features, including shifts of sex ratio to about 90% females (Deason and Hile 1947; Brown 1970). The bloater observation plotted represents average growth and age at first reproduction across 10 years (Fig. 2a), but co-hort-specific observations may be particularly important for studying this species. When more data are available for these and other deep-water fishes, it may be also appropriate to treat them separately with a distinct predictive relation.

The other two outliers are yellow perch populations that mature at age 4. Yellow perch is a typical warm-water species. Other warm-water fishes studied here include white perch and gizzard shad (Appendix A). When t_R is less than 4, values for those warm-water fishes including yellow perch overlap with cool-water invertebrate-eating fishes in our regressions (Figs. 2a-2b). If we separate warm-water populations as a subgroup including those yellow perch that matured at age four, the relation between *K* and t_R is linear rather than a power function, and R^2 with six populations is 0.98 (Fig. 2c). More data are needed to clarify whether yellow perch alone are distinct or if they might belong to another functional category with other species.

For the eight populations of walleye, age at first reproduction (t_R) can be predicted using L_{int} , and R^2 for the predictive relation is 0.90 (Fig. 2*d*). Two data points are just outside of the confidence limits. They may be related to differences in natural mortality, but more data are needed to test the idea. Statistically, we could exclude those two data points as outliers, but prediction residuals for those data points are still less than 1.

Applications of the index for growth–reproduction linkage

The index for growth-reproduction linkage (eq. 13) is applicable to both invertebrate-eating populations and walleye populations. For invertebrate-eating fishes (Fig. 3*a*), the plot of I_{G-R} versus t_R can be modeled as $I_{G-R} = 0.88t_R - 1.04$, with R^2 of 0.99. For populations of walleye (Fig. 3*b*), the plot of I_{G-R} versus t_R can be modeled as $I_{G-R} = 0.41 t_R + 0.87$, and R^2 is 0.91. The difference between these two *b* values for eq. 13 is 0.46 and is statistically significant (df = 23, p < 0.0001). Correspondingly, the intercept for invertebrate-eating fishes is negative, whereas the intercept for walleye is positive. In our previous study on lake trout (He and Stewart

Fig. 2. Predicting age at first reproduction (t_R) using the von Bertalanffy growth coefficient (*K*) or the Ford–Walford intercept (L_{int}). Data are in Table 1 and Appendix A. (*a*) The relation between $\ln(t_R)$ and $\ln(K)$ for 11 species of invertebrate-eating fishes with 23 populations. Four data points are outliers because they are far outside of confidence intervals. See more details in text. (*b*) The relation between t_R and *K* for 19 populations of invertebrate-eating fishes. Outliers identified in (*a*) are not included. (*c*) The relation between t_R and *K* for a potential subgroup with six populations of warm-water invertebrate-eating fishes, including yellow perch, white perch, and gizzard shad. (*d*) The relation between t_R and L_{int} for eight populations of walleye.



2001), the regression line was $I_{G-R} = 0.42 t_R + 1.01$, which is very similar to that for walleye populations studied here.

Discussion: body-growth comparisons and their life-history implications

As commonly interpreted, a phase of fast growth often means relatively large size at a given age. Alm (1959) indicated that he used such a notion because he had no better choice. We need to be aware of the vagueness of the commonly used notion of fast growth, slow growth, or no difference in growth. When age is larger than 1, body size at a given age may not be a clear indicator of growth rates or growth condition because it includes effects of previous life stages. Particularly, young-of-the-year growth, yearling growth, and the remaining juvenile-adult growth often have different intrinsic features and are related to different environments (e.g., Balon 1975). To compare body growth, we often need to compare body-growth trajectories with one or another growth model. Using the conventional expression of the von Bertalanffy growth model, however, we often have difficulties drawing clear biological implications, although statistical comparisons can be rigorous. Biological meanings of the model structure and parameters have to be fully clarified.

The biological basis of the von Bertalanffy growth model has been studied mostly from an energetic perspective (von Bertalanffy 1938; Pauly 1981). Along this line, the model can always be criticized for its assumptions, such as scaling body mass to body length cubed, scaling anabolism to twothirds the power of the body mass, and considering catabolism as a constant proportion of body mass. It is important to understand the energetic basis of a body-growth trajectory (e.g., He and Stewart 1998), but the above sufficient energetic assumptions for the VBGM are all unrealistic and are not necessary. The model has been independently developed by emphasizing proper description of body-growth trajectories (Brody 1927; Ford 1933; Walford 1946). In this paper, we completed the idea of Ford (1933) and Walford (1946), and used three measurable stage-specific variables (L_1, ρ_v, ρ) to express the commonly used von Bertalanffy growth model (eqs. 3-5). Changes in each of these three variables may have different relative dominances, and each of them can lead to a major change in size at ages (eq. 5). Other possible sets of parameters cannot represent distinguishable life stages, so growth comparisons may be improved by focusing on the three major stage-specific variables or elements.

Fig. 3. General linkages between body growth and age at first reproduction. The index of the *y* axis (I_{G-R}) is defined by the left side of eq. 13 and related explanatory text. It represents an intrapopulation linkage or the linkage between body length and age at first reproduction with a given growth trajectory. A complete plot represents interpopulation linkage. With substantial changes in values of growth parameters, the interpopulation linkage between body length and age at first reproduction is representative of many growth trajectories. Data are in Table 1. Outliers identified in Fig. 2*a* are not included. (*a*) Populations of invertebrate-eating fishes. (*b*) Populations of walleye. The differences between populations of invertebrate-eating fishes and walleye are statistically significant (see text).



As with this paper, the conventional expression of the von Bertalanffy growth model (eqs. 1-2) will be used continuously on its own right, but biological meanings of von Bertalanffy growth parameters can be better understood from an alternative perspective. It is confusing to use the coefficient K to denote fast growth or slow growth because there are contrasting stage-specific effects on that coefficient. With similar asymptotic size, a relatively smaller Ford–Walford slope (ρ) or larger K (eq. 8) is due to a relatively larger L_1 or ρ_v that leads to relatively larger sizes at young ages (eq. 5). With similar sets of L_1 and ρ_y , however, a relatively smaller ρ or larger K is associated with a relatively smaller asymptotic size, which indicates poor growth condition and rapid decreases in growth rates during the final growth stanza. Precisely, K should be formally named as a coefficient for decay of annual growth rate (Pauly 1981). With a given asymptotic size, a rapid decrease in growth rate must be positively related to a rapid growth in young age, so we have $E/K = L_{inf}$ (see eq. 1 and documenta-

tion of its parameters), but a relatively large K always indicates a rapid decrease in annual growth rate.

It is also confusing to use K to discuss the trade-off between growth rate and life span. The positive relation between K and mortality has been well documented (Pauly 1980; Charnov 1993; Jensen 1996), but it should not be explained only in a hypothetical way. The dimension of K is t^{-1} , but it is not a growth rate in the sense of per capita increment per time or increment per time (eq. 1). When a relatively large K is associated with relatively higher mortality, underlying mechanisms may include at least the following contrasting effects from different life stages. A small p or large K often indicates poor growth conditions in the final growth stanza, and poor growth condition is often associated with high mortality. When best-growing individuals are selectively removed by predation or fishing, survivors will have a relatively smaller asymptotic size with a relatively larger K. When a small ρ or large K is resulting from a relatively larger yearling size (L_1) or a high relative growth rate of a yearling (ρ_{y}) , there may be subsequent high mortality because of stresses related to early age at first reproduction.

In this paper, we have emphasized that age at first reproduction is predictable using K or L_{int} . A rapid decrease in annual growth after age two may lead to a small ρ or large K and is associated with early age at first reproduction. The result is consistent with the idea that high mortality favors early age at first reproduction (Roff 1984), because unfavorable growth condition and high mortality often happen in concert. For the same reason, when slow growth in the first two years of life leads to small size at subsequent ages and a late age at first reproduction, it is also consistent with the idea that high mortality in early life favors delayed age at first reproduction (Stearns 1992).

We hope that more comparative studies will be conducted and published with a focus on cohort life histories and individual variations. It is fortunate that there have been many well-documented studies in the Great Lakes. Most of those studies are landmarks of fish biology in this region. Early techniques for identifying fish ages may have involved some bias, especially in analyzing very old fishes, but it is hard to imagine that various independent studies reported here can lead to arbitrary relations between growth parameters and age at first reproduction. Future studies may explore other typical cases with the same species or other species similar to those studied here. We believe that they will also confirm the general results in this paper, because our empirical analysis is built on a solid theoretical basis.

When body length shows a normal growth pattern, the von Bertalanffy growth model is typically one of the best models (Ricker 1979; Chen et al. 1992). General linkages between age at first reproduction and growth trajectories are also theoretically sound (Stearns 1992) and empirically well known (Beverton 1992; Shuter et al. 1998; He and Stewart 2001). Additional complexities are related to various combinations of different effects from major life stages (Hutchings 1993; Jonsson and Jonsson 1993; Fox 1994). The three major life stages (represented by L_1 , ρ_y , and ρ) have contrasting effects on growth potential, *K* and L_{int} . They also have contrasting relations to t_R . Implementation of accurate predictive functions calls for consideration of factors that may influence body growth during various life stages in different ways. Those factors include types of ecosystems, trophic positions, environmental conditions, and spatial heterogeneity. With consideration for all of those complexities, our approach can be tested at various levels, including individual, population, and interspecific comparisons. Such an approach may represent a new perspective for studying fish population dynamics and changes in relative dominance of fish species (e.g., Shuter et al. 1998).

In the Great Lakes, changes in the fish communities have been well documented (e.g., Smith 1968; Christie 1974). More attention is needed to consider that the two upper levels of food webs in the Great Lakes have been operating with relatively short life spans. For Coregonus, Prosopium, and other native invertebrate-eating fishes, age at first reproduction has a range from 2 to 12. First reproduction at age 4-7 is very common. Predation pressure on those native fishes is normally on immature age classes (Smith 1968). Exotic species such as alewife and rainbow smelt are now among the dominant secondary consumers in all of the lakes. They mostly reach their first reproduction at age 2–3 with relatively smaller sizes. For those exotics and small native species, predation pressure is on both immature and mature age classes. There have been similar changes in life histories of piscivorus fishes. Introduced Pacific salmons reach their first reproduction at age 2-4, much younger than the native lake trout, although similar to burbot (Lota lota). All of those changes in age at first reproduction, or successes of fishes with notably different life histories, are associated with their body-growth trajectories. Together, they also have substantial impacts on food-web dynamics and related ecosystem stability. The results of our study have the following implications. For piscivorus fishes, early life growth often has a dominant effect on life history. For hatcherysupported populations with artificially large yearlings, however, potential reductions in asymptotic size may have longterm effects on restoration of naturally reproducing and selfsustaining populations. For secondary consumers, growth potential after age 1 or age 2 is the dominant factor influencing life histories. Rebuilding populations of native fishes that attain relatively larger sizes and spawn at later ages might improve food-web and ecosystem stability.

For harvested fish populations and their prey, the following potential mechanisms deserve further studies and clarifications. When best-growing and large-sized individuals are selectively removed, overall effects of harvests or predation may include three major outcomes. One is a selection for enhanced body growth in the first 2 years of a life, which allows for early age at first reproduction. Such an outcome is likely not sustainable in many natural ecosystems because it requires a very stable ecosystem with high productivity. The second outcome is a selection for survivors with poor growth after age 2, which is also associated with early age at first reproduction. Such an outcome leads to undesirable dominance of small-sized species or populations. It also leads to unstable food webs because both premature and mature fish may be vulnerable to predation. The third outcome is a potential increase in asymptotic size and age at first reproduction due to reductions in intra- and inter-specific competition among fishes of age 2 and older. The last potential outcome is dangerous because delayed reproduction during periods of overexploitation might lead to sudden collapse of fish populations. The above three outcomes are likely to confound each other. Using a stage-explicit perspective to analyze cohort life histories may be an important contribution to improving our understanding of complex fish population dynamics.

Acknowledgments

We thank Bob O'Gorman for comments on an early draft. This paper is a result of research funded by the National Oceanic and Atmospheric Administration (NOAA) award NA86RG0056 to the Research Foundation of State University of New York for New York Sea Grant. The U.S. Government is authorized to produce and distribute reprints for government purposes notwithstanding any copyright notation that may appear hereon. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies.

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Appendix A.

The von Bertalanffy growth model for each of the following populations was estimated by this study (Table 1).

Table A1. Length at age data for 28 fish populations.

		Body length at ages (mm)											
Reference	Species	1	2	3	4	5	6	7	8	9	10	11	12
Van Osten and Hile 1949	Osten and Hile 1949 Lake whitefish		323	409	460	498	526	544	561	579	589	602	615
Van Osten 1939	Lake whitefish	127	226	312	409	488	544	582	607	630	643	658	676
Mraz 1964 <i>a</i>	Lake whitefish	168	300	406	480	523	559	582	607	625			
Dryer 1963	Lake whitefish	130	203	277	338	381	424	465	508	544	561		
Edsall 1960	Lake whitefish	140	183	213	239	257	274	292	307	328	345	366	391
Bailey 1963	Round whitefish	117	183	231	274	307	333	356	376	394			
Mraz 1964b	Round whitefish	117	229	312	361	399	447	472	498				
Armstrong et al. 1977	Round whitefish	139	255	346	396	436	460	481					
Eschmeyer and Bailey 1954	Pygmy whitefish	46	69	88	107	117	123	130					
Dryer and Beil 1964	Lake herring	119	188	239	282	307	333	343					
Dryer and Beil 1968	Bloater	99	150	183	208	226	239	254	269	285	297		
Deason and Hile 1947	Kiyi	124	173	218	241	259	267	272	274				
Brown 1972	Alewife	97	144	165	177	185	194						
Bronte et al. 1991	Alewife	89	156	176	189	188							
O'Gorman et al. 1997	Alewife	89	131	153	161	164	169						
Norden 1967	Alewife	94	140	159	173								
Bailey 1964	Rainbow smelt	66	150	193	221	239	257						
Bodola 1965	Gizzard shad	140	285	335	366	390							
Jobes 1952	Yellow perch	94	170	216	241	264	279						
El-Zarka 1959	Yellow perch	69	109	150	191	224	259	282					
Hile and Jobes 1942	Yellow perch	71	117	163	203	229	264	287					
Wells 1983	Yellow perch	85	167	227	261	288	310	326					
Schaeffer and Margraf 1986	White perch	78	171	210	239								
Wolfert 1969, 1977	Walleye	213	371	454	513	563	607	649	683	722	760		
Hile 1954	Walleye	163	305	414	480	541	582	617	645	668			
Priegel 1969	Walleye	152	257	338	394	439	480	511	536				
Eschmeyer 1950	Walleye	125	239	315	368	414	455	480	503	518	533		
Smith and Pycha 1961	Walleye	142	211	267	310	345	379	401	424	452			

Note: All body lengths are total body length.