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Long-term patterns in growth of Oneida Lake walleye: a multivariate and stage-explicit approach for applying the von Bertalanffy growth function

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Total length (L_T) and its inter annual variation of walleye *Sander vitreus* from Oneida Lake, New York, based on 51 years (1950–2000) of data for ages 1 to 7 years were analysed. Growth increased over time at young ages, did not change at intermediate ages and decreased at old ages. Total length at age increased over time to age 4 or 5 years, but was stable at older ages. Principle component analysis was used to study the pattern of variations in annual L_T increments among years. More than 92 and 91% of inter annual variability in growth was described by the first three principal components for males and females, respectively. The first principal component was a general indicator of annual growth at all ages, but was dominated by annual growth at intermediate ages. The second and third principal components represented contrasts among yearling L_T, yearling growth and growth at older ages. Therefore, changes in the three stage-specific parameters, yearling L_T, yearling growth and asymptotic L_T, explained most of the variance in observed growth. Using these three stage-specific parameters for the von Bertalanffy growth function facilitated interpretations of growth comparisons.

Key words: growth; inter annual variations; Oneida Lake; principal component analyses; von Bertalanffy growth function; walleye.

INTRODUCTION

It is often difficult to detect or interpret growth changes in fish populations (Živkov *et al.*, 1999), despite substantial modifications of aquatic food webs, dramatic depletions of fishery resources and noticeable changes in fish life histories (Hilborn *et al.*, 1995; Jennings & Kaiser, 1998; Pauly *et al.*, 1998). Part of this difficulty is associated with standard parameters of the von Bertalanffy growth function as a basis for growth comparisons (von Bertalanffy, 1938). For example, the 'growth' coefficient K in the von Bertalanffy equation is neither annual growth nor per

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capita growth per year. A large K could result from rapid growth in young ages or from a small asymptotic length (He & Stewart, 2002). The non-zero parameter t_0 is an 'age' for body length of zero, and reflects both transformations and aggregations of various measurable elements in a growth trajectory. Combinations of von Bertalanffy growth parameters (Gallucci & Quinn II, 1979; Pauly, 1981; Moreau, 1987) or multivariate analyses of those parameters (Misra, 1980; Bernard, 1981; Cerrato, 1990) have not overcome these difficulties.

He & Stewart (2002) suggested the use of an alternative formulation of the von Bertalanffy growth function, based on inputs of yearling length, yearling growth and the slope of the Ford-Walford plot, which is the average proportion of annual growth that can be maintained at each age interval after age 2 years (Ford, 1933; Walford, 1946; Ricker, 1979; King, 1995). This new formulation can be derived from the traditional von Bertalanffy growth function (Schnute & Fournier, 1980; He & Stewart, 2002), but has the advantage that each parameter represents a directly interpretable stage in the growth of the animals. It separates growth into three stages: growth to age 1 years (yearling length), growth between age 1 and age 2 years (yearling growth) and growth of older fishes. For this approach to be used in growth comparisons, however, it must capture all major variations in growth of a fish population. To test applicability of this alternative formulation of the von Bertalanffy growth function, as a basis for growth comparison, a long-term data set of back calculated growth of walleye *Sander vitreus* (Mitchell) from Oneida Lake, New York, 1950–2000, was analysed.

The walleye has been the dominant predator in Oneida Lake since the early 1940s, and there have been continuous yearly records for age and growth since 1945 (Forney, 1965, 1980). This population may be one of the most comprehensively studied walleye populations anywhere, and there is a wealth of information on the lake environment, food web interactions and population dynamics (Forney, 1980; Mills & Forney, 1988; Rose *et al.*, 1999). Similar to fishes in many freshwater and marine ecosystems, this population has been affected by fishery harvests, hatchery operations, invasive species, changes in nutrient loading and other human impacts (Forney, 1965, 1977; Rutherford *et al.*, 1999; Mayer *et al.*, 2000; Idrisi *et al.*, 2001; VanDeValk *et al.*, 2002; Rudstam *et al.*, 2004). Those ecosystem changes probably have had impacts on walleye growth or observed size at age during the past 60 years, which in turn could have influenced life-history features and population dynamics (Craig *et al.*, 1995; He & Stewart, 2001, 2002).

Principal component analysis (PCA) was used to examine the inter annual variability in length increment during each age interval of walleye. The method is conceptually simple and provides an objective basis for identifying the primary sources of variance based on the raw data. Chen & Mello (1999) applied a similar method to study growth of cod *Gadus morhua* L. Following the analysis of He & Stewart (2002) and their use of the von Bertalanffy growth function, the main principal components for this walleye data set should represent contrasts between yearling length, yearling growth and growth at older ages.

MATERIALS AND METHODS

To describe growth of Oneida Lake walleye, walleye total length (L_T) data for 51 years (1950–2000) were used. Total lengths were backcalculated from scale annuli, based on the standard Fraser-Lee method (DeVries & Frie, 1996) and an empirical intercept of 57 mm (Forney, 1965). Walleye were captured during gillnet surveys in the summer and autumn, except for the first 9 years in which samples were collected during spring spawning. Detailed sampling procedures are given by VanDeValk *et al.* (2002). Forney (1965) found no difference in backcalculated L_T between spring and autumn caught individual fish. Average numbers of fish aged per year was 720 (range 187 to 1252) with approximately equal numbers of males and females. The oldest age included in the analyses was age 7 years, which was often the maximum age for reliable scale interpretation. Otoliths and scales gave the same age readings for fish up to 7 years (A.J. VanDeValk, unpubl. data).

To model the average growth pattern, two alternative formulations of the von Bertalanffy growth function were used. Both were fitted to the data using non-linear regression with Marquardt option (SAS NLIN procedure, SAS, 1999). The first formulation was the commonly used equation (von Bertalanffy, 1938):

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

where, L_t is body length at age t (years), L_∞ is asymptotic length, K is a growth coefficient and the parameter t_0 is a hypothetical age for body length of zero. The second formulation was a different form of the same growth model (Schnute & Fournier, 1980; He & Stewart, 2002):

$$L_t = L_1 + p_y L_1(1 - p^{t-1})(1 - p)^{-1}. \tag{2}$$

Here, a growth curve starts with yearling length, L_1. When age t equals 2 years, $L_2 = L_1 + p_y L_1$, and p_y is the relative growth rate of a yearling. When age is >2 years, there is a simple geometric progression involving the Ford–Walford slope, which is defined by $p = (L_{t+1} - L_t)(L_t - L_{t-1})^{-1}$, and $p = e^{-K}$. When age t is infinitely large, the term of $(1 - p^{t-1})$ can be eliminated and the resultant length is L_∞.

One of the reasons for using two identical equations is to demonstrate implications of using equation 1. As an approximation of equation 1, the well known Ford–Walford plot of L_{t+1} and L_t normally does not include a full expression of yearling length and yearling growth and, therefore, corresponds only to a special case of the von Bertalanffy growth function with zero value for the parameter t_0 (Ricker, 1979; King, 1995). Equation 2 represents completion of the Ford-Walford plot when there are sufficient data. The complete plot should have: 1) yearling length (L_1) on the y axis, 2) the relative growth rate of a yearling (p_y) as the first slope and 3) the Ford-Walford slope as the second slope (He & Stewart, 2002). All conventional von Bertalanffy growth parameters in equation 1 can be calculated from variables in equation 2 (Schnute & Fournier, 1980; He & Stewart, 2002). In contrast to the expression of equation 1, however, equation 2 clearly implies that variations in a growth trajectory stem from variations in yearling length, yearling growth and an average proportional decline in growth rate with age after 2 years.

To assess the implications provided by equation 2 and embodied in equation 1, the patterns of inter annual growth variation of Oneida Lake walleye were analysed. PCA was conducted on annual L_T increments for ages 0 to 7 years. Data were grouped by year, and analysed separately for males and females. All analyses were conducted using SAS PRINCOMP procedure with the option of covariance matrix (SAS, 1999). The covariance option emphasized variables with the largest variation, which was correct when all input variables were in the same units (mm). Linear regressions were used to determine potential trends of growth over years (SAS REG procedure, SAS, 1999).

RESULTS

The average growth of Oneida Lake walleye during the 51 years (1950–2000) was well described by either equation 1 or 2 (Table I). Asymptotic length of males (432 mm L_T) was smaller than that of females (477 mm L_T), but there were no significant differences in yearling length and yearling growth between

TABLE I. Estimated parameters for the von Bertalanffy growth function fitted to male and female Oneida Lake walleye using both equations 1 and 2 (see text)

	Females			Males		
	Estimate	95% CL		Estimate	95% CL	
Equation 1						
L_∞	477·7	466·8	488·6	431·5	424·8	438·3
K	0·340	0·312	0·368	0·400	0·374	0·426
t_0	−0·264	−0·366	−0·162	−0·189	−0·271	−0·107
Equation 2						
L_1	166·9	162·2	171·6	163·4	159·6	167·3
G	89·6	85·3	93·9	88·5	84·8	92·1
p	0·712	0·692	0·731	0·670	0·653	0·688

L_1, yearling length (mm); G, yearling growth $(L_2 - L_1) = (p_y L_1)$; p, Ford–Walford slope; L_∞, asymptotic length (mm); K, von Bertalanffy growth coefficient (year^{-1}); t_0, hypothetical age (year) for body length of zero.

males and females (Table I). Males and females also had different Ford-Walford slopes (p) and growth coefficients (K), but no significant differences in the parameter t_0 (Table I).

There were time trends in inter annual growth variations, and these trends differed among age groups (Table II). Yearling length increased over years ($n = 51$, $r^2 = 0{\cdot}13$ for males and 0·15 for females, $P < 0{\cdot}01$). Yearling growth also increased over years ($n = 51$, $r^2 = 0{\cdot}22$ for males and 0·19 for females, $P < 0{\cdot}001$). Growths at intermediate ages (2–3 years for females, 2–4 years for males) were stable. Growths at older ages decreased. For examples, annual growth from age 5 to age 6 years of both males and females decreased over years ($n = 51$, $r^2 = 0{\cdot}11$ for males and 0·08 for females, $P < 0{\cdot}05$). Consequently, L_T at ages 1–4 and 1–5 years increased for females and males, respectively, but the increasing trend no longer existed by age 5 years for females and by age 6 years for males (Fig. 1 and Table II). At older ages L_T were relatively stable.

The first three principal components expressed all interpretable growth variations in the PCA results (Table III). The first principal component explained 66 and 71% of inter annual growth variation for males and females, respectively; the second principal component explained 17 and 14%, respectively; and the third principal component explained 9 and 6%, respectively. Overall, the first three principal components explained 92 and 91% of inter annual growth variation for males and females, respectively.

The first three principal components in turn were dominated by variations in yearling length, yearling growth and growth >age 2 years. The first principal component was a general indicator for annual growth at every age, but it was dominated by annual growth at intermediate ages. It had significant positive relations with L_T increments at every age ($P < 0{\cdot}004$), and coefficients of the linear relation were summarized as the eigenvector (Table III). The second

TABLE II. Mean growth (mm) and total length (mm) at age for ages 0–7 year walleye from Oneida Lake, New York, 1950 to 2000. Slopes and their *P*-values are from regression analyses of time trends

	Growth			L_T		
Age (years)	Mean	Slope	*P*	Mean	Slope	*P*
Female						
0	168	0·289	0·005	–	–	–
1	87	0·593	0·002	168	0·289	0·005
2	67	NS	NS	254	0·901	<0·001
3	47	NS	NS	321	0·548	<0·001
4	32	−0·268	0·050	367	NS	0·002
5	23	−0·221	0·048	398	NS	NS
6	18	−0·239	0·016	420	NS	NS
7	–	–	–	437	NS	NS
Male						
0	164	0·295	0·009	–	–	–
1	87	0·605	<0·001	164	0·295	0·009
2	63	NS	NS	250	0·902	<0·001
3	41	NS	NS	312	0·921	<0·001
4	25	NS	NS	352	0·588	<0·001
5	18	−0·216	0·020	377	0·357	0·004
6	14	NS	NS	394	NS	NS
7	–	–	–	408	NS	NS

NS, no significant change over time.

principal component indicated the contrast between annual growth before age 2 years and annual growth at older ages (Table III). It had significant negative relations with annual growth before age 2 years ($P < 0.003$), and significant

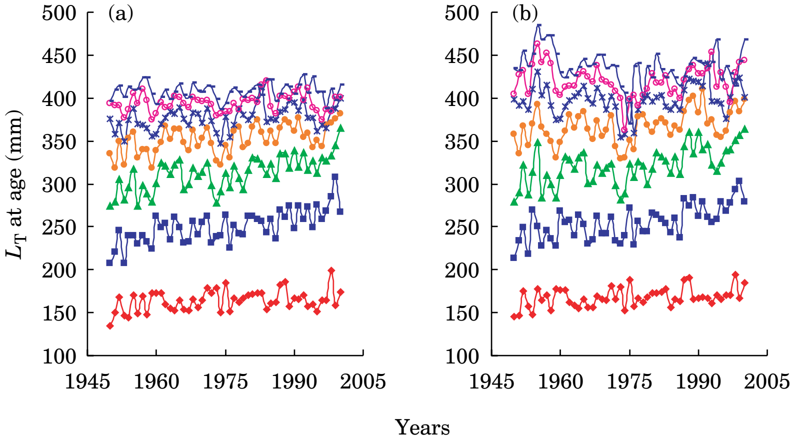

FIG. 1. Total length at age for ages 1 (◆), 2 (■), 3 (▲), 4 (●), 5 (✳), 6 (○) and 7 (▬) year (a) male and (b) female walleye from Oneida Lake, 1950–2000.

TABLE III. Eigenvectors of the first three principal components and their correlation coefficients with total length increments at ages 1–7 year (LI_age) of walleye in Oneida Lake, New York, 1950–2000

	Females			Males		
	Principal component			Principal component		
	1	2	3	1	2	2
Eigenvectors and their explained proportions (italics) of the total variance						
LI_1	0·134	−0·382	0·846	0·190	−0·345	0·904
LI_2	0·525	−0·670	−0·201	0·549	−0·696	−0·322
LI_3	0·470	−0·010	−0·354	0·491	0·111	−0·217
LI_4	0·464	0·301	−0·022	0·451	0·399	0·113
LI_5	0·384	0·302	0·181	0·359	0·267	0·068
LI_6	0·302	0·278	0·204	0·261	0·349	0·111
LI_7	0·179	0·383	0·211	0·145	0·177	0·056
	0·709	*0·140*	*0·059*	*0·658*	*0·170*	*0·090*
Correlation coefficients and their probability for the H_O of no correlation						
LI_1	0·399	−0·506	0·728	0·447	−0·414	0·789
	0·004	0·0002	<0·0001	0·001	0·0026	<0·0001
LI_2	0·852	−0·483	−0·0939	0·823	−0·529	−0·179
	<0·0001	0·0003	0·512	<0·0001	<0·0001	0·210
LI_3	0·937	−0·0091	−0·203	0·933	0·107	−0·153
	<0·0001	0·950	0·152	<0·0001	0·455	0·284
LI_4	0·928	0·267	−0·0125	0·885	0·398	0·0819
	<0·0001	0·0579	0·931	<0·0001	0·0038	0·568
LI_5	0·882	0·308	0·120	0·868	0·328	0·0605
	<0·0001	0·0279	0·403	<0·0001	0·0188	0·673
LI_6	0·848	0·348	0·165	0·752	0·511	0·118
	<0·0001	0·0124	0·246	<0·0001	0·0001	0·410
LI_7	0·561	0·533	0·190	0·558	0·347	0·080
	<0·0001	<0·0001	0·181	<0·0001	0·0126	0·576

positive relations with annual growth >age 3 years ($P < 0·03$). The third principal component emphasized variation in yearling L_T, which was not correlated with yearling growth and annual growth of older fish (Table III). This principal component only had significant positive relation with yearling L_T ($P < 0·0001$).

The first three principal components summarized time trends of inter annual growth variation involving all age groups (Fig. 2). The first principal component for both males and females fluctuated over years without a trend. This suggests that growth of Oneida Lake walleye has been relatively stable over this time period. There were significant time trends, however, in the second principal component for both males and females ($n = 51$, $r^2 = 0·59$ for males and 0·68 for females, $P < 0·0001$). These trends resulted primarily from the long-term increase in yearling L_T and yearling growth but also from the decrease in growth at older ages (Tables II to III). The third principal component fluctuated without a time trend. This was in contrast with the second principal component,

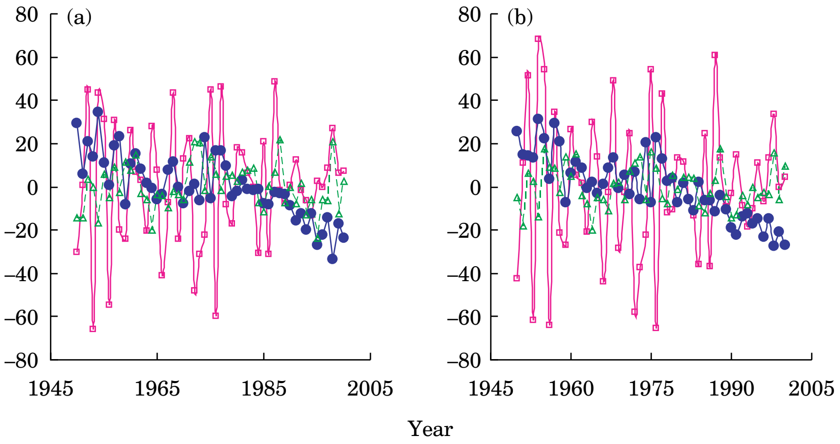

FIG. 2. The first three principal components [1 (□), 2 (●) and 3 (△)] plotted with years, for the growth of (a) male and (b) female walleye in Oneida Lake, New York.

but the third principal component only represented those variations in yearling L_T that were not correlated with increased yearling growth or decreased growth of older fish.

DISCUSSION

Growth models should have parameters that are easy to use for interpreting growth variation. The PCA indicated that the inter annual variations and time trends in the growth of Oneida Lake walleye were explained by variations in yearling L_T, yearling growth and growth after age 2 years. This suggests that the three stage formulation of the von Bertalanffy growth function was adequate for expressing average growth and explaining most of the inter annual growth variations observed in the lake. The parameter of L_∞ is directly related to growth after age 2 years when yearling length and yearling growth are given (equation 2), $L_{\mathrm{inf}} = L_1 + (L_2 - L_1)\,(1 - p)^{-1}$. Variance in the Ford-Walford slope (p) and the von Bertalanffy growth coefficient (K) did not add new information once L_∞ was used with L_1 and L_2, because $K = -\ln(p)$ and $p = (L_\infty - L_2)\,(L_\infty - L_1)^{-1}$. Variance in the parameter t_0 is composed of the variances in a number of measurable variables, because $t_0 = 1 - \ln[p_y(1 + p_y - p)^{-1}]\,[\ln(p)]^{-1}$ (Schnute & Fournier, 1980; He & Stewart, 2002). It may be difficult to statistically relate variations in K and t_0 to the environment, because they involve more than one transformation as well as aggregations of different measurable components of a growth trajectory. In contrast, variations in yearling length, yearling growth and asymptotic length are readily interpretable and can be correlated with environmental changes.

Growth in the first year is probably governed by different factors than growth in older age classes (Hile, 1941). In a long-term fishing experiment on perch *Perca fluviatilis* L. in Windermere, LeCren (1958) found dramatic increases in growth after age 2 years with no comparable changes in growth during the first two years of life. Forney (1965, 1966), who analysed the earlier years of the present data set, showed differences in factors affecting growth of yearling and older walleye. Similar observations have been made for walleye elsewhere (Smith & Pycha, 1960; Madenjian, 1991; Staggs & Otis, 1996; Quist *et al.*, 2003). In the present study, clear time trends of increasing yearling L_T and yearling growth and of decreasing growth at older ages were found (Tables II to III and Figs 1 and 2). Increasing yearling size has also been observed for yellow perch *Perca flavescens* (Mitchill) in Oneida Lake in the 1990s and attributed to both density-dependent growth and clearer water associated with the zebra mussel *Dreissena polymorpha* (Pallas) invasion in 1992 (Mayer *et al.*, 2000). In addition, there were inter annual differences in growth rates of Oneida Lake walleye that affected all age classes. These differences were probably related to density of forage fishes in the lake (Forney, 1965, 1980).

The present analyses were based on observed growth of fish caught in gillnet surveys. The lack of increase in annual growth at older ages could be due to higher fishing mortality of rapid-growing and larger fish. A decreasing trend in back calculated L_T at age associated with the age of the fish at the time of capture (the Lee phenomena, Lee, 1920), however, was not observed, which would have been expected if the samples were biased towards slower growing older fish.

Using growth parameters in growth comparison is always associated with the difficulties dealing with size effects on growth rates. Various authors have attempted to overcome this problem by using allometric equations (Jobling, 1983), residual analysis (Mayer *et al.*, 2000), focusing on linear growth periods (Olson *et al.*, 2001) or explicit comparisons of length at age for several age classes (Muth & Wolfert, 1986). It is always possible to compare growth or length at all ages (Quist *et al.*, 2003), but a synthesis based on simple growth parameters is preferable. Many studies have used aggregates of von Bertalanffy parameters for growth comparisons (Gallucci & Quinn II, 1979; Pauly, 1981, 1991), or used multivariate comparisons based on those parameters (Misra, 1980; Bernard, 1981; Cerrato 1990). Živkov *et al.* (1999) criticized almost all commonly used growth parameters and indices.

The present approach is an extension of Hile's (1941) work. Hile (1941) found that variation in yearling length was independent of variation in growth at older ages, making it necessary to separately compare yearling lengths and length increments at a given older age interval. The present PCA results and the use of the von Bertalanffy growth function extended Hile's (1941) method in two ways. First, yearling growth was considered as a transition period to allow for statistics on situations where yearling length and subsequent growth were controlled by different factors. Second, asymptotic length was used to reflect growth condition after age 2 years because body length or length increment after age 1 year may confound different effects from earlier-age and later-age growth. Both yearling length and yearling growth from equation 2 and asymptotic length from equation 1 were used to facilitate interpretation. Asymptotic length can be calculated from equation 2, but it is easier to obtain its confidence limits by fitting equation 1 to the data; the same is true for yearling length and yearling growth with equation 2.

In other systems, growth can be more complex than that of Oneida Lake walleye. For example, Persson *et al.* (2000) showed a change in growth patterns after *P. fluviatilis* became piscivorous. Many salmonids have different growth patterns in rivers compared with the ocean (Crisp, 1999). In such cases, stage-specific variables in equation 2 can be modified such that the first stage represents a body length at an age older than 1 year (Schnute, 1985), or it may be necessary to use more complex growth models (Richards, 1959; Taylor, 1962; Schnute, 1981), including a separation of von Bertalanffy growth curves for different growth stanzas (Soriano *et al.*, 1992; Ross *et al.*, 1995). Principal component analyses can probably be used to identify major sources of variation in non-linear growth trajectories, and to help select the proper growth model for a given data set.

The connections and trade-offs between growth comparisons using highly aggregated and transformed parameters and using stage-specific parameters may largely stem from the von Bertalanffy growth coefficient K. As commonly used, K is a curvature parameter indicating how fast a fish approaches its asymptotic length; but it has been called a growth parameter, growth coefficient, growth constant and even growth rate, simply because it happens to have a unit of (t^{-1}). Those terminologies have reflected loose and often misleading interpretations that a large K indicates rapid growth. A typical example is that the combination of (KL_∞) has been interpreted as the growth rate at the birth of an animal (Gallucci & Quinn II, 1979; Lai *et al.*, 1996). By its formal definition K actually is a coefficient for the decay of annual growth. It is the negative natural logarithm of the average proportion that annual growth can be maintained at each age interval (Ford, 1933; Walford, 1946; Ricker, 1979; King, 1995); it is proportional to a catabolic coefficient (von Bertalanffy, 1938; Pauly, 1981); and it is a 'deceleration' coefficient when the decrease of specific growth rate is a linear function of itself (Schnute, 1981; Wootton, 1998). To reconcile the formal definition of K with its curvature property and its common usage as a growth parameter, it is beneficial to have the discrete and difference form of the von Bertalanffy growth function with stage-specific growth parameters (equation 2) and have the complete Ford-Walford plot that has yearling length on the y axis (He & Stewart, 2002).

Proper descriptions of growth variations are important for understanding population dynamics. Specifically, the age of maximum biomass depends on growth and mortality rates (Deriso, 1987). Over the past 50–60 years, Oneida Lake walleye have had similar L_T at age 6 years, but yearling L_T and yearling growth have increased, and annual growth >age 4 years has decreased. For female walleye at an observed adult mortality rate of *c.* $Z = 0{\cdot}29$ (25% per year, Rudstam *et al.*, 2004), the age for maximum biomass is *c.* 4·5 years based on the growth parameters in Table I. Given the observed range of yearling L_T (123–195 mm), and the range of yearling growth (40–145 mm), and assuming a constant L_∞, growth coefficient K has a range of 0·13–0·57, and the age for maximum female biomass has a range of 3·4–6·6 years. Those inter annual or inter year-class variations in the age at maximum population biomass and their relations with environmental variables will be easier to interpret and predict when stage-explicit parameters are used.

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