A Comparison of von Bertalanffy and Polynomial Functions in Modelling Fish Growth Data

Y. Chen, D. A. Jackson, and H. H. Harvey

Department of Zoology, University of Toronto, Toronto, Ont. M5S 1A1, Canada

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We compared the von Bertalanffy growth function (VBGF) and five polynomial functions (PF) in modelling fish growth for 16 populations comprising six species of freshwater fishes. Ranked results of the variance explained by each growth function indicated that VBGF described growth data better than three- and four-parameter polynomial functions. Log-transforming length and age greatly improved the goodness-of-fit of the three-parameter polynomial function. Statistical comparison of growth between populations or sexes was done using a general linear model for polynomial functions. An analysis of residual sum of squares was proposed to compare the resultant VBGFs because the nonlinear formulation of the VBGF prevented traditional analysis of covariance procedures. Fitting of different growth functions to the same growth data set yielded the same result in the intraspecies growth comparisons for three species (eight populations) but different results for two species (seven populations). Where ages of the fish were less than the maximum age in the samples, *dL/dt* were similar for all growth functions except the parabola based on the log-transformation of length alone. The VBGF proved to be the best growth model for all 16 populations.

Nous avons comparé la fonction de croissance fondée sur l'équation de von Bertalanffy et cinq fonctions polynomiales appliquées à la modélisation de la croissance des poissons dans le cas de 16 populations (six espèces) de poissons dulcicoles. D'après le classement des résultats de la variance par rapport à chaque fonction de croissance, la fonction de croissance reposant sur l'équation de von Bertalanffy fournit un meilleur tableau des données sur la croissance que les fonctions polynomiales à trois et à quatre paramètres. La transformation logarithmique des données sur la longueur et l'âge a grandement amélioré la qualité d'application de la fonction polynomiale à trois paramètres. Nous avons procédé à une comparaison statistique de la croissance entre les populations ou les sexes au moyen d'une modélisation linéaire générale pour les fonctions polynomiales. Nous avons proposé d'analyser la somme des carrés obtenue, dans le but de comparer les résultats reposant sur l'équation de von Bertalanffy, car la formulation non linéaire de ce type de fonction nous empêchait de faire l'analyse de covariance classique. En comparant les données sur la croissance à l'intérieur d'une même espèce, l'application de diverses fonctions de croissance au même ensemble de données a abouti aux mêmes conclusions chez trois espèces (huit populations), mais les résultats différaient chez deux autres espèces (sept populations). Lorsque l'âge des poissons était inférieur à l'âge maximal des échantillons, les rapports *dL/dt* étaient semblables pour toutes les fonctions de croissance, exception faite de la parabole représentant la transformation logarithmique de la longueur seulement. La fonction de croissance fondée sur l'équation de von Bertalanffy s'est avérée le meilleur modèle de croissance des 16 populations étudiées.

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Fish growth data are usually fitted by an appropriate mathematical function to generalize the growth process, predict the growth trend, and compare the growth patterns between populations or species (Rao 1958; Moreau 1987). Of the mathematical functions applied to fish growth, the von Bertalanffy growth function (VBGF) (Ricker 1975; Pauly 1979; Moreau 1987) is used most widely by fisheries scientists. However, polynomial functions (PF) are being used with increasing frequency (e.g. Rafail 1972; Geoghegan and Chittenden 1982; Standard and Chittenden 1984; Chen et al. 1988), and they have been suggested to replace the VBGF in describing fish growth (e.g. Knight 1968; Roff 1980). Nevertheless, in recognition of the fact that even equivalent growth functions can produce divergent predictions of fish growth behaviour, it may be misleading to choose a function a priori without systematic comparison. Unfortunately, few such comparisons have been made between VBGF and PFs.

Fitting different growth functions to the same growth data set can yield different results and interpretations in the comparison of fish growth. For this reason, statistical comparisons are important when modelling fish growth data. However, despite the importance of testing the concordance between different mathematical functions fitted to the same growth data, few studies have considered this issue.

In this study, based on the growth data of six fish species differing greatly in growth, VBGF and five PFs were compared with respect to (1) goodness-of-fit, (2) the suitability and concordance of the statistical test, (3) reliability of coefficient estimates in the growth functions, and (4) the underlying implication of the growth functions in terms of growth rate in length as *dL/dt*.

Materials and Methods

Six fish species were collected from eight Ontario lakes and one Manitoba lake for this study (Table 1). Age of white sucker (*Catostomus commersoni*) was determined using the finray method (Beamish and Harvey 1969). Scales were employed to

TABLE 1. Information on species included in this study.

Species	Population	Sexed	Sample size	Plotted in Fig. 1
Pike	Wellman	Yes	31	Females
Pumpkinseed	Crosson	No	155	No
	Plastic	No	146	Yes
	Heeney	No	153	No
Rock bass	Plastic	No	181	Yes
Walleye	Wellman	Yes	174	Females
White sucker	Barry	Yes	41	Females
	Bentshoe	Yes	86	No
	Crosson	Yes	108	No
	Dickie	Yes	165	No
	McQuaby	Yes	92	Females
	Red Chalk	Yes	133	No
Yellow perch	Crosson	No	149	No
	Plastic	No	44	No
	Heeney	No	103	No
	Wellman	No	125	Yes

TABLE 2. Growth functions compared in this study.

Name	Mathematical expression
VBGF	$L_t = L_\infty \cdot (1 - \exp(-K \cdot (t - t_0)))$
PF 1	$L_t = a + b \cdot t + c \cdot t^2$
PF 2	$L_t = a + b \cdot \log_{10}(t+1) + c \cdot (\log_{10}(t+1))^2$
PF 3	$\log_{10} L_t = a + b \cdot \log_{10}(t+1) + c \cdot (\log_{10}(t+1))^2$
PF 4	$\log_{10} L_t = a + b \cdot t + c \cdot t^2$
PF 5	$L_t = a + b \cdot t + c \cdot t^2 + d \cdot t^3$

derive the age data for pumpkinseed (*Lepomis gibbosus*), yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), and walleye (*Stizostedion vitreum*). Northern pike (*Esox lucius*) ages were based on both opercular bones and scales.

The VBGF is expressed as $L_t = L_\infty \cdot (1 - \exp(-K \cdot (t - t_0)))$, in which L_t is length-at-age, L_∞ is the asymptotic length, K is Brody growth coefficient, and t_0 is the age at which length is 0 (Ricker 1975). Standard nonlinear optimized techniques of curve fitting were used to estimate the coefficients and their associated standard error (Gallucci and Quinn 1979; Vaughan and Kanciruk 1982; Cerrato 1990).

A general polynomial function is usually expressed as:

$$f(x) = a + b \cdot x + c \cdot x^2 + \ldots + k \cdot x^n \quad (k \text{ not equal to } 0)$$

in which $f(x)$ is a PF of degree (or order) n in the variable x. In particular, quadratic and cubic functions are the forms usually employed in fisheries (e.g. Knight 1968; Rafail 1972; Roff 1980). Four three-parameter polynomial functions were derived for this study (Table 2). In PF 2 and PF 3, t was replaced by $t + 1$ prior to a logarithmic transformation in order to calculate dL/dt for all ages. A four-parameter polynomial function was also included in this study (Table 2).

Because lengths-at-age of fishes at different age classes were derived from different sample sizes, data were weighted by the sample size to accurately represent length data for different age groups. To standardize the goodness-of-fit comparison, fitting of both PFs and VBGF was done using nonlinear optimization methods (Gauss–Newton method, NLIN of SAS Institute 1985). The measure of goodness-of-fit chosen was r^2.

The r^2 values were ranked among the different growth functions for each population with the largest r^2 as 1, second largest as 2, and so on. A nonparametric test (Friedman 1937, 1940) was employed on the ranked results of r^2 to test the significance of the goodness-of-fit comparisons among growth functions. Friedman's test statistic, χ_r^2, was calculated with a correction for tied ranks (Zar 1984). The association of rank ordering of r^2 values among growth functions was measured nonparametrically by the Kendall coefficient of concordance, ω (Kendall and Babington-Smith 1939; Kendall 1962). The distribution of χ_r^2 was considered to approximate the χ^2 distribution with $a - 1$ degrees of freedom. For this study, factors of the test (i.e. a) equal the number of the selected functions whereas blocks are the number of fish populations (Zar 1984). Pairwise comparisons of the goodness-of-fit also were made between growth functions.

Because of the nonlinear formulation of the VBGF, a general linear model could not be used for an analysis of covariance (ANCOVA). Instead, an analysis of the residual sum of squares (ARSS) was employed to compare VBGF between the sexes and among populations (Ratkowsky 1983). Procedures of the ARSS were as follows: (1) residual sum of squares (RSS) and an associated degree of freedom (DF) of VBGF were calculated for each sample, (2) the resultant RSS and DF of each sample were added to yield summed RSS and DF, (3) data of all samples were pooled to calculate the RSS and DF of a total VBGF, and (4) the F-statistic was calculated as

$$F = \frac{\dfrac{\mathrm{RSS}_p - \mathrm{RSS}_s}{\mathrm{DF}_{\mathrm{RSS}_p} - \mathrm{DF}_{\mathrm{RSS}_s}}}{\dfrac{\mathrm{RSS}_s}{\mathrm{DF}_{\mathrm{RSS}_s}}} = \frac{\dfrac{\mathrm{RSS}_p - \mathrm{RSS}_s}{3 \cdot (\mathrm{K}-1)}}{\dfrac{\mathrm{RSS}_s}{N - 3 \cdot K}}$$

where RSS_p = RSS of each VBGF fitted by pooled growth data, RSS_s = sum of the RSS of each VBGF fitted to growth data for each individual sample, N = total sample size, and K = number of samples in the comparison. This method was modified from the ARSS developed for the comparison between linear models (Zar 1984). To test whether there was a difference

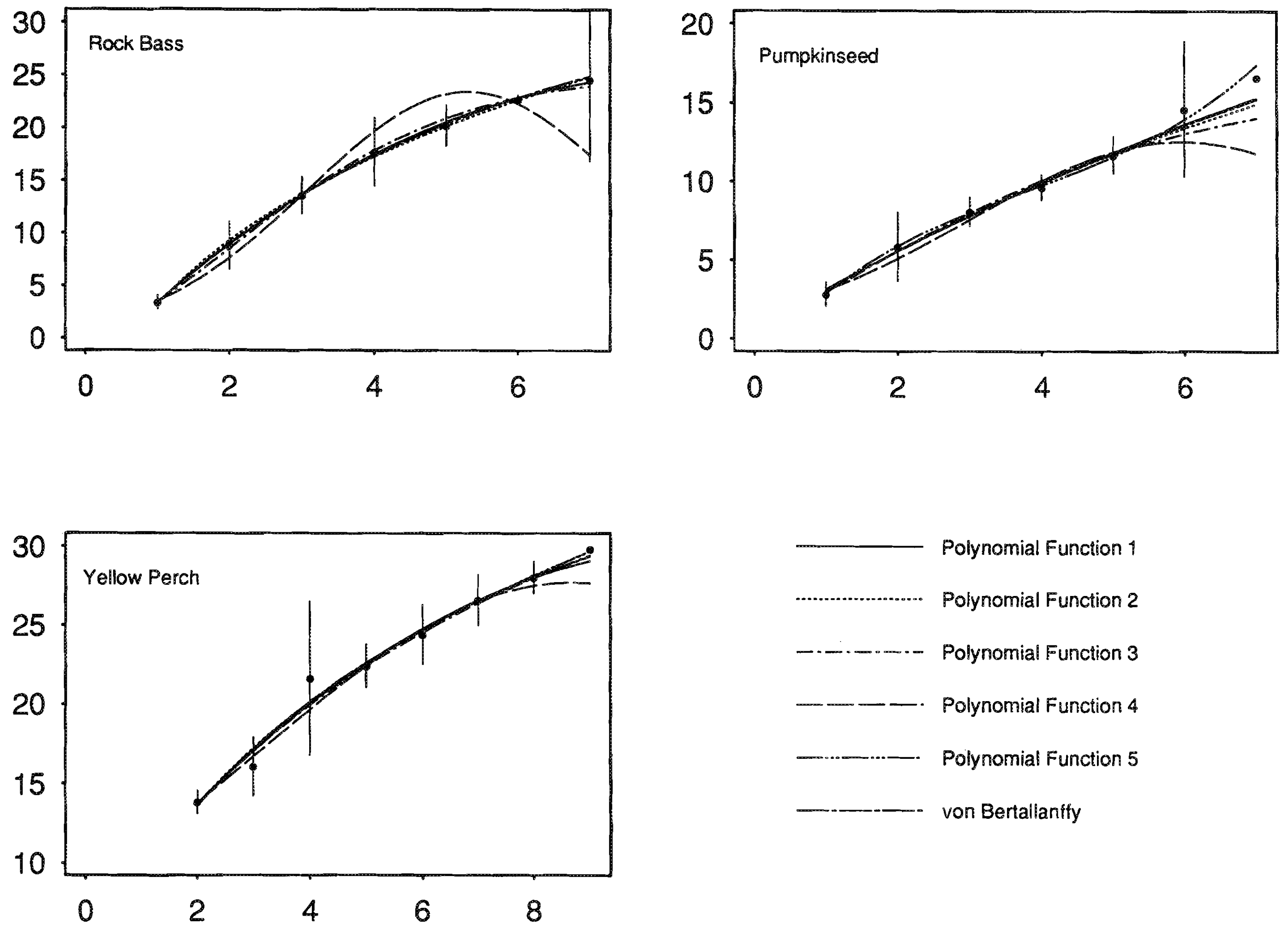

FIG. 1. Length-at-age curves for six fish species with the tested mathematical functions applied. Abscissa, fish age (yr); ordinate, fish fork length (cm); vertical bars, standard errors. (*Fig. 1 concluded next page*)

TABLE 3. Sum of r^2 ranks for each growth function. Numbers in parentheses are average ranks which equal the ratio of the sum of ranks over number of fish populations or sexually differentiated populations.

Species	VBGF	PF 1	PF 2	PF 3	PF 4	PF 5
Northern pike	3	10	7	6.5	12	3.5
	(1.50)	(5.00)	(3.50)	(3.25)	(6.00)	(1.75)
Pumpkinseed	4	15	10	10	18	6
	(1.33)	(5.00)	(3.33)	(3.33)	(6.00)	(2.00)
Rock bass	1	3	5	4	6	2
	(1.00)	(3.00)	(5.00)	(4.00)	(6.00)	(2.00)
Walleye	3	10	10	4	10	5
	(1.50)	(5.00)	(5.00)	(2.00)	(5.00)	(2.50)
White sucker	22	53.5	47	28.5	70	31
	(1.83)	(4.46)	(3.92)	(2.38)	(5.83)	(2.58)
Yellow perch	6	18	16	15	20	9
	(1.50)	(4.50)	(4.00)	(3.75)	(5.00)	(2.25)
Sum	39	109.5	95	68	136	56.5
	(1.63)	(4.56)	(3.96)	(2.83)	(5.67)	(2.35)

in VBGF between the samples, the calculated F value was then compared with the critical F, with the DFs of numerator and denominator equal to $3\cdot(K - 1)$ and $N - 3\cdot K$, respectively. The ANCOVA was used for the PFs between the sexes and among populations (PROC GLM) of SAS Institute 1985). The results of the statistical comparison using ARSS and ANCOVA on VBGF and PFs were compared to determine whether there were substantial differences in growth associated with the use of these different growth functions.

Parameters of each growth function were tested for all populations to find how many were not significantly different from 0. The growth rate in length as dL/dt is an underlying consequence of a growth function. Examination of differences in dL/dt between growth functions may help to explain the dif-

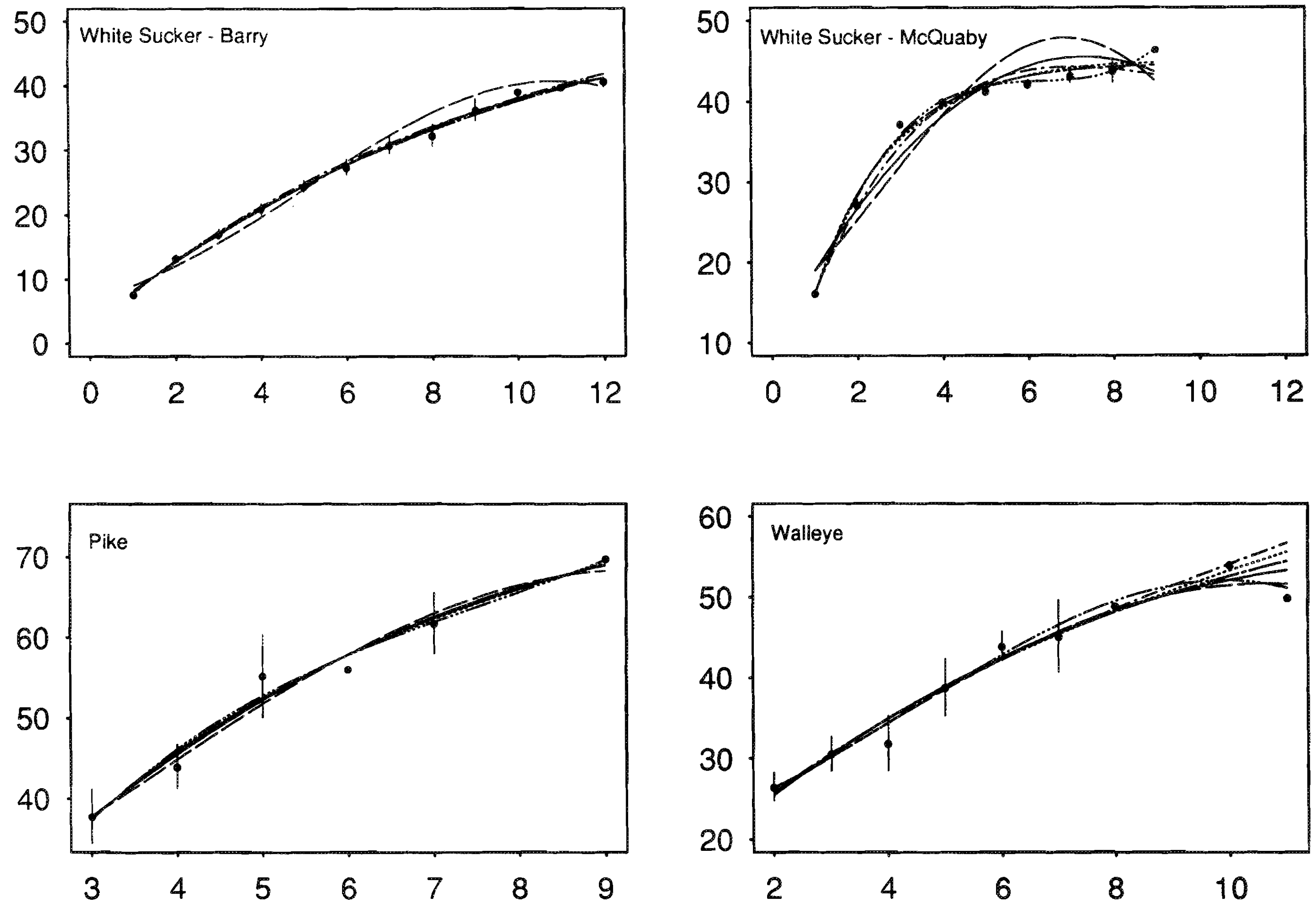

FIG. 1. (*Concluded*)

TABLE 4. Friedman's χ^2 and Kendall's coefficient of concordance, ω, for the pair comparisons between functions. Numbers above and below the diagonal are Friedman's χ^2 and Kendall's ω, respectively. *The function from the column heading has a significantly better ranking of r^2 values than the function identified in the corresponding row; **the function from the row heading has a significantly better ranking of r^2 values than the function identified in the corresponding column.

Function	VBGF	PF 1	PF 2	PF 3	PF 4	PF 5
VBGF		20.2**	16.7**	8.2**	24.0**	6.0
PF 1	0.8403		2.7	16.7*	16.7**	24.0*
PF 2	0.6944	0.2500		4.2	10.7**	10.7*
PF 3	0.3403	0.6944	0.1750		20.2**	0.7
PF 4	1.0000	0.6944	0.4458	0.8403		20.2*
PF 5	0.1736	1.0000	0.4458	0.0292	0.8403	

ferences in goodness-of-fit between these functions. The dL/dt derived from the different growth functions were examined using growth data of two white sucker populations with the high and low growth rates. Length-at-age and six fitted functions (VBGF plus five PFs) were plotted for populations of each species to illustrate the variations in growth among the six fish species.

Results

Goodness-of-Fit Comparison

A plot of length-at-age and six fitted growth functions for populations of each species (Table 1) showed that there were great differences in growth among fish species (Fig. 1). The VBGF had smallest r^2 ranks for all six species (Table 3). The magnitudes in r^2 ranks in decreasing order were VBGF, PF 5, PF 3, PF 2, PF 1, and PF 4. Considering the tied rank groups in each block, Friedman's χ_r^2 statistic is 77.7 (n = 24). This was significant at the 5% level (i.e. χ^2 = 11.07, DF = 5), indicating a significant difference in the rank ordering of the r^2 values among the growth functions. Kendall's coefficient of concordance was 0.648 (n = 24), indicating good agreement in the r^2 ranks for the different populations (i.e. blocks).

Based on paired comparisons between the VBGF and each PF, the VBGF was significantly better than PFs in goodness-of-fit (Tables 3 and 4). However, there were multiple comparisons here, and the selected significance level should be adjusted. According to the Bonferroni method, significance level of 0.05 was divided by number of the functions involved in the comparisons, equalling 0.0083 (Miller 1977). The calculated level of significance between VBGF versus PF 5 was 0.0159 (Table 4), greater than the required adjusted p value of 0.0083. Therefore, there were no significant differences between the VBGF versus PF 5. Similarly, there were no significant differences in the goodness-of-fit between PF 5 and PF 3 ($p > 0.5$). However, PF 5 was significantly better than PF 1 ($p < 0.001$), PF 2 ($p = 0.001$), and PF 4 ($p < 0.001$) (Table 4). PF 3 fitted the growth data significantly better than PF 1 ($p < 0.001$) and PF 4 ($p < 0.001$), but had no significant difference with PF 2 ($p = 0.045$, which was greater than the required significance level using a Bonferroni adjustment, i.e. $p = 0.0083$). There were no significant differences in r^2 ranks between PF 1 and PF 2, but both fit significantly better than PF 4 (Tables 3 and 4). Consequently, in terms of the goodness-of-fit, VBGF was best, PF 3 and PF 5 were second best, and PF 4 was the worst for the growth data of this study (Tables 3 and 4). The better fit provided by PF 5 relative to other PFs is not unexpected given that PF 5 contains a third-order term not present in other PFs.

Suitability and Concordance of the Statistical Test

ARSS on the VBGF indicated that growth of white sucker from six populations differed significantly between the sexes and among populations (Table 5). There were significant differences in growth modelled by the VBGFs among the populations of pumpkinseed and among the populations of yellow perch (Table 5). No significant differences in VBGFs were found between the sexes for walleye and northern pike (Table 5).

Statistical analysis for the polynomial growth functions was done using ANCOVA to determine whether significant differences in growth existed between the sexes or among populations. The ANCOVAs for each of the five PFs indicated that there were significant differences in growth of white sucker between the sexes. Significant differences also were found among populations for both females and males. For pumpkinseed, the ANCOVAs indicated that there were significant differences among populations in growth modelled by PF 3, but not by the other four PFs. Significant differences among populations were not found in the growth of yellow perch modelled by PF 2, but were by the other four PFs. From the ANCOVAs on each of the PFs, it may be concluded that there were no significant differences between the sexes in the growth of both walleye and northern pike.

Reliability of Coefficient Estimates in the Growth Functions

Estimates of L_∞ for the fishes in this study were close to the observed maximum length. The coefficient K in all resultant VBGFs was between 0 and 1, and 16.7% of the estimates of t_0 were significantly greater than 0.

For polynomial growth functions, the number of samples with parameters significantly different from 0 was greater for the parabolas based on the log-transformation of length and both length and age (i.e. PF 3 and PF 4) than with the other PFs. For parameter d of the PF 5 (Table 2), 50% of the estimates were not significantly different from 0, indicating that the cubic factor in the function might not contribute substantially in fitting the growth data.

Implication of the Growth Functions

Female white sucker of the McQuaby population grew extremely rapidly when they were young (Fig. 2a). The growth rate in length as dL/dt was shown to be very similar among the growth functions except dL/dt derived from PF 4 between ages 2 and 8 (Fig. 2a). However, after age 8, only the VBGF described the growth rate as asymptotic to 0. For slow-growth females of the Barry population, dL/dt derived from all functions except PF 4 were similar until age 10, but after that, dL/dt of growth functions diverged. With the increase of age, VBGF tended to be the only function that could meaningfully describe the change of growth rate in length with age (Fig. 2b). The variability in dL/dt among growth functions was large for young fish (i.e. before age 2), especially in the McQuaby population with its high growth rate in length (Fig. 2a).

Discussion

Since the shape of the growth curve for fishes may vary between populations or species, the growth function that provides the best representation of growth data may vary also. Therefore, it is essential to assess the goodness-of-fit in any comparison among growth functions. The great difference in growth among these six species and the results of the comparison of goodness-of-fit indicate that the VBGF shows greater flexibility in describing growth data than the three- and four-parameter PFs. The three-parameter PF using log-transformed data for length-at-age and age explained the growth data better than those with log-transformation of only one variable or without logarithmic transformation (Tables 3 and 4). A four-parameter PF only described the growth data to a similar degree as the three-parameter PF with logarithmic transformation of length-at-age and age (Tables 3 and 4). However, when the significance level was adjusted according to the Bonferroni method (Miller 1977), differences in goodness-of-fit became nonsignificant between VBGF and PF 5. This result might suggest that although the VBGF is better than PF 5 in goodness-of-fit (Table 3), the differences between them were not great (Table 4). However, there are four parameters being estimated in PF 5, more than the parameters (i.e. three) in VBGF. It is

TABLE 5. Species comparison of growth modelled by VBGF by means of RSS. Rock bass was unsexed and had only one population available; thus, no statistical comparison was done for it.

Species	Comparison between	RSS_p	DF	RSS_s	DF	F	Pr > F
Northern pike	Sexes	110.55	9	105.53	6	0.10	>0.5
Pumpkinseed	Populations	206.86	16	30.39	10	9.68	0.0011
Walleye	Sexes	330.29	18	323.85	15	0.10	>0.5
White sucker	Populations (F)	32761.9	71	980.99	56	121.0	<0.0001
	Populations (M)	22588.8	66	221.18	51	343.8	<0.0001
	Sexes	59747.1	140	55350.7	137	3.63	0.0161
Yellow perch	Populations	1830.8	31	293.8	25	12.79	<0.0001

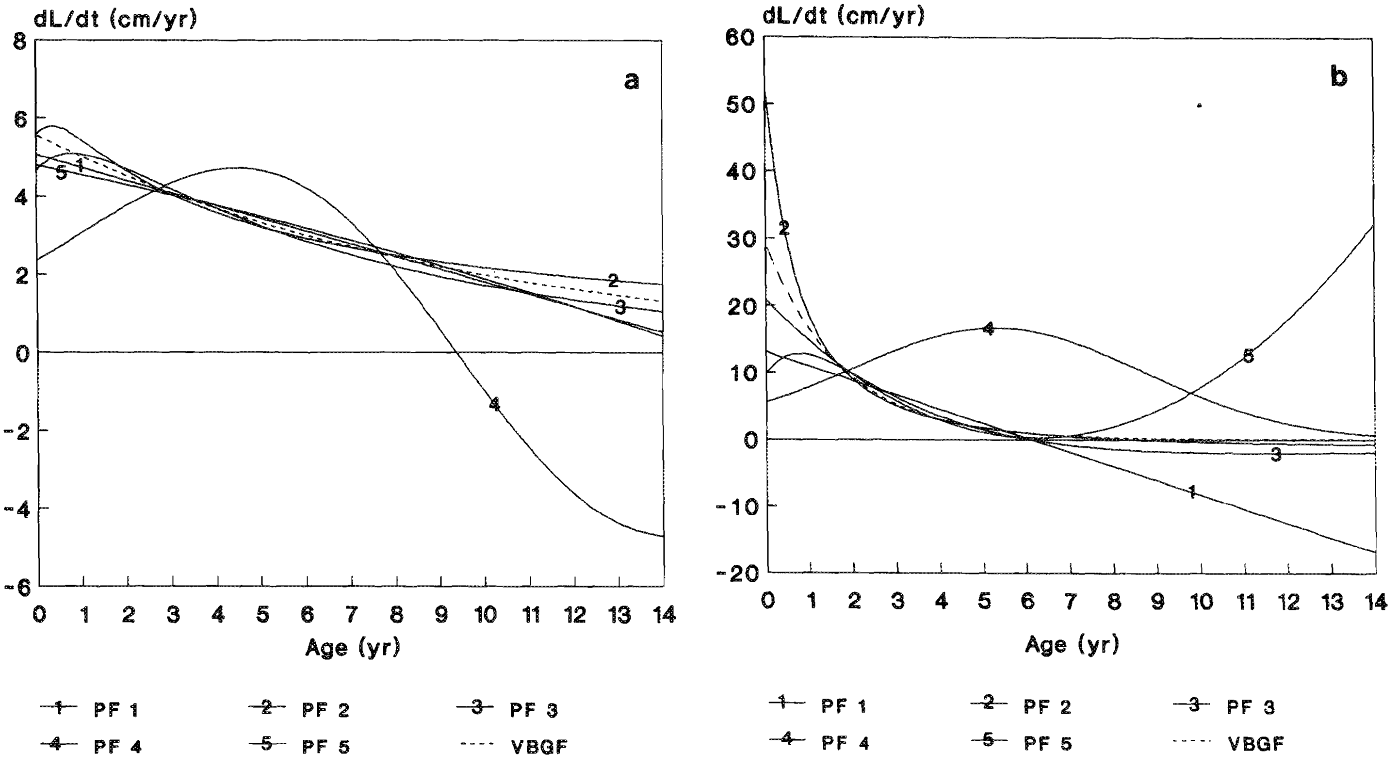

FIG. 2. Growth rate in length as *dL/dt* for female white sucker in (a) Barry Lake and (b) McQuaby Lake.

well known that there is a better chance of explaining more variance if more parameters are included in the function. If VBGF was compared with the PFs having the same number of parameters (i.e. three), it remained significantly better in goodness-of-fit after adjusting the level of the significance. Log-transformation of data is able to make the data more similar in magnitude, and perhaps reduces data-effect error (i.e. residual SS; Kimura 1990). Also, since there were no significant differences between PF 3 and PF 5, when a PF is used for fitting growth data, PF 3 may be the best choice in terms of goodness-of-fit.

Commonly used linear methods allowing statistical comparison of growth data (i.e. ANCOVA or ANOVA) cannot be employed on the VBGF because of its nonlinear formulation and high degree of correlation between its three parameters (Kingsley 1979; Gallucci and Quinn 1979; Misra 1980; Cerrato 1990). Two general approaches are usually suggested for the growth comparison of the VBGF. One is to test individual parameters (Gallucci and Quinn 1979; Kingsley 1979; Pauly 1979; Misra 1980; Bernard 1981). The other is based on likelihood ratio statistics (Kimura 1980; Kirkwood 1983; Cerrato 1990). However, there are many theoretical and practical problems in employing these two approaches (see Moreau 1987; Cerrato 1990). ARSS is informative and easy to calculate and for simplicity was used in the comparison of growth modelled by a VBGF.

Statistical comparisons for both PFs (based on ANCOVA) and VBGF (based on ARSS) showed that there were significant differences between the sexes and among populations for six populations of white sucker (Table 3). There were also no substantial differences in growth comparison for white sucker or between the sexes for both northern pike and walleye using PFs or VBGF. However, in the comparisons of pumpkinseed growth from three populations, substantially different conclusions were drawn from using different functions. Significant differences in growth were found among populations if the growth data were modelled by the VBGF and PF 3, but the differences in growth were not found if other PFs (i.e. PF 1, 2, 4, or 5) were used. This function-selection-related difference in the results of growth comparisons was also observed for yellow perch. If growth data of yellow perch were fitted to PF 2, ANCOVA indicated that there were no significant differences among populations. However, if other PFs or VBGF were employed, significant differences were found by using the ANCOVA or ARSS. Thus, it is apparent that selection of different functions in describing fish growth may affect the results in growth comparisons (i.e. the power of the test between populations/sexes is influenced by the choice of growth functions). Recognizing this, caution is warranted in selecting a mathematical expression for fish growth data if the ultimate purpose of setting up a growth model is to compare growth between samples. We suggest that statistical comparisons be done for each of the functions selected.

Kohn (1986) stressed that if parameter values were estimated by formal optimization methods, it was essential to show that these estimates were reasonable and reliable for the biological data that the model was explaining. Therefore, in keeping with this view of the estimates of VBGF parameters, L_∞ should be reasonably close to the maximum fish length in the sample (Taylor 1958; Pauly 1979; Moreau 1987), t_0 should be smaller than 0 so that fish at age 0 could have a positive length (Moreau 1987), and K might vary between 0 and 1 for fishes with long life spans (Pauly 1978). However, for PFs, there are no such criteria for judging the acceptability of the parameter estimates. Advocates of the PFs emphasize their mathematical simplicity rather than their biological usefulness.

Small differences between estimates of L_∞ and observed maximum length indicated that the estimated L_∞ values were reasonable (Taylor 1958; Pauly 1979; Moreau 1987). Coefficient K in resultant VBGFs ranged from 0 to 1, indicating that these VBGFs were probably reasonable in describing growth data. Although 16.7% of the resultant t_0 estimates were significantly greater than 0, the exact value of t_0 is not usually considered to be important or necessary for some methods using t_0, such as (1) yield per recruit computation, (2) use of length-converted catch curves for Z evaluations, and (3) length-based cohort analysis (Moreau 1987).

Large standard errors associated with the parameters may limit the ability to detect a significant difference between the parameters and 0, thus reducing the power of the tests. Those factors (i.e. t, t^2, etc.) with parameters not significantly different from 0 were neither essential nor useful in describing the variance of the dependent variable (i.e. L_t). The number of parameter estimates significantly different from 0 in VBGF and PF 3 was substantially more than that in other PFs. This suggests that VBGF and parabolas with log-transformation of both length and age were better than other PFs in terms of reliability of the estimates of function parameters.

The general process of fish growth (where it is considered impossible that fishes will have negative growth rate in length) is well known; thus, it is more sensible to use the first derivative of growth functions (dL/dt) than growth functions themselves to judge whether the functions are reasonable in describing fish growth dynamics. dL/dt derived from PF 1 represents a straight line, meaning the growth rate in length changed constantly with age t. This pattern of growth rate might be true in the early life of fish or for short-lived fish (e.g. Nikolskii 1969; Standard and Chittenden 1984) but is not true for growth patterns of the entire life of long-lived fish (e.g. Nikolskii 1969; Kozlowski and Uchmanski 1987; Hayes and Taylor 1990). dL/dt derived from other PFs is parabolic curves related, indicating that there is a maximum or minimum dL/dt. Thus, if the growth process of fish is described by this function, two growth stages are included: increase and decrease in growth rate. This type of growth pattern often occurs in weight growth of fishes rather than in length growth (Nikolskii 1969).

Growth rates asymptotic to 0 are thought to accurately represent the growth of long-lived fish (e.g. Nikolskii 1969; Kozlowskii and Uchmanski 1987; Chen et al. 1988; Murphy and Taylor 1989). Mathematically, it is obvious that no PF can describe this process. The plots of dL/dt on age for the two white sucker populations clearly illustrate this condition (Fig. 2), showing great differences between the trajectories of dL/dt derived from the PF 4 versus other functions. However, these differences are not great in the plot of L_t on age (Fig. 1). This indicates that differences in dL/dt trajectory are more apparent than those in length-at-age trajectory between growth functions. Therefore, plotting dL/dt may simplify the detection of differences between growth functions relative to the differences displayed in plots of L_t alone (Fig. 1 and 2).

The rate of growth in length as dL/dt derived from the VBGF realistically defined the patterns of fish growth in length. Based on the nonparametric analysis of r^2 ranks, the VBGF described the growth data better than three- and four-parameter PFs in this study. Before selecting the growth function for a growth data set, a systematic comparison should be done among growth functions being considered for use.

We sugget that VBGF be selected as the most suitable growth function for the six species in this study. If PFs must be chosen, we suggest the parabola with log-transformation of both dependent and independent variables.

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