

Back-Calculation of Fish Length from Scales: Empirical Comparison of Proportional Methods

CLAY L. PIERCE

National Biological Service, Iowa Cooperative Fish and Wildlife Research Unit
Department of Animal Ecology, 7 Science II, Iowa State University, Ames, Iowa 50011, USA

JOSEPH B. RASMUSSEN

Department of Biology, McGill University
1205 Avenue Dr. Penfield, Montreal, Quebec H3A 1B1, Canada

WILLIAM C. LEGGETT

Department of Biology, Queens University
Kingston, Ontario K7L 3N6, Canada

Abstract.—We compared three proportional back-calculation methods for scales using data sets for pumpkinseeds *Lepomis gibbosus* and golden shiners *Notemigonus crysoleucas* from 10 southern Quebec lakes, and we validated back-calculations by comparing them with observed lengths at time of annulus formation. Ordinary least-squares regression (OR) was compared with geometric mean regression (GMR) for describing body–scale relationships. Although minor differences were detected in body–scale regressions among lakes, pooling data across lakes yielded linear body–scale relationships with very high r^2 . Differences between OR and GMR body–scale relationships were negligible in both species. Likewise, all back-calculation methods produced equivalent results. Back-calculated lengths generally corresponded well with observed lengths in all pumpkinseeds age-classes and in golden shiners older than 1 year. Observed lengths were often greater than back-calculated lengths for age-1 golden shiners. Our results, indicating little or no difference among methods, contradict recent reviews claiming substantial disagreement among methods. Tighter body–scale relationships in our data sets than in previous studies appear to explain this contradiction. We suggest that tight body–scale relationships are attainable for many species, obviating concern over which proportional back-calculation method is chosen.

Growth is an important aspect of the ecology and life history of fish, and quantification of growth is frequently a crucial part of fisheries research and management (Summerfelt and Hall 1987; Weatherley and Gill 1987). Back-calculation of lengths from scales is a widely used approach for estimating the growth history of individual fish and characterizing the growth of fish populations (Jearld 1983; Carlander 1987; Busacker et al. 1990). Back-calculation of lengths from scales relies on recognition of annual growth markings (annuli) on scales to calculate an estimated body length associated with each annulus. Body lengths estimated in this way make up a growth history, from which growth rate can be inferred.

Since first being introduced by Lea (1910) nearly a century ago, many back-calculation methods have been proposed and used (Francis 1990). The recent review by Francis (1990) covered 54 studies published since 1978 that used back-calculation. Five forms of body–scale relationships were used, four kinds of regression were used to describe these relationships, and six back-calculation meth-

ods were used to estimate lengths. Some of this variety in methodology is clearly warranted by circumstance. For instance, species exhibiting non-linear body–scale relationships require a different method than those whose body–scale relationship is linear. Back-calculations based on otoliths or other structures present at hatching may require a different method than those based on scales, which typically appear at some time after hatching (Schramm et al. 1992). However, much of this diversity in methods reflects historical inertia, disagreement on the theoretical merits of different approaches, and ignorance of some of the available techniques (Francis 1990). The lack of conformity in back-calculation also introduces unnecessary confusion and perhaps reduces confidence in back-calculation results because it is unclear how closely results of different methods correspond.

The purpose of this study was to empirically compare several back-calculation methods for scales applied to common data sets and to validate back-calculations by comparing them with observed lengths at time of annulus formation. We

used similar data sets for two species, one with ctenoid and the other with cycloid scales. The data sets were collected at the same time by consistent methods in 10 lakes.

We have not attempted an exhaustive comparison of all available methods and variations. Several authors (Carlander 1981; Gutreuter 1987; Francis 1990; Schramm et al. 1992) have refuted the general class of techniques known as "regression" methods on both theoretical and empirical grounds. Use of this approach apparently persists due to its intuitive simplicity and to ignorance of its shortcomings. In this study we focused on the general class of techniques known as "proportional" methods. Specifically, we examined the Fraser-Lee method because of its popularity (Busacker et al. 1990; Francis 1990) and two lesser-known proportional methods because of their professed theoretical merits (Francis 1990). In addition, we compared ordinary least-squares regression with geometric mean regression (Ricker 1992) for calculating the intercept parameter used in the Fraser-Lee equation.

Methods

Study lakes and species.—We conducted this study in 10 lakes located in the Eastern Townships region of southern Quebec. Locations, littoral fish communities, and other characteristics of these lakes were described by Pierce et al. (1994 and references cited therein). Pumpkinseeds *Lepomis gibbosus* and golden shiners *Notemigonus crysoleucas* are common and widely distributed littoral zone fishes in North America (Scott and Crossman 1973; Lee 1981). Together, they account for 30% of the littoral zone fish biomass and are among the most abundant littoral species in our study lakes (Pierce et al. 1994). Pumpkinseeds have ctenoid scales; golden shiners have cycloid scales.

Fish sampling.—Using beach seines as described by Pierce et al. (1990), we sampled pumpkinseeds and golden shiners from each of the 10 lakes in spring (9 May to 20 May) and again in late summer (8 September to 22 September) of 1988. These samples were collected as part of a larger sampling effort to quantify the biomass and community characteristics of all littoral fish species in these lakes (Pierce et al. 1994), as well as growth (C. L. Pierce, unpublished) and condition (Liao et al. 1995) of pumpkinseeds and golden shiners.

Captured fish were anesthetized immediately in 2-phenoxyethanol, put on ice, and frozen within a few hours. In the laboratory, length-stratified ran-

dom subsampling yielded at least 50 fish of each species from most combinations of lake and sampling date. The fish were individually weighed (wet) to the nearest 0.01 g on an electronic balance and measured (total length) to the nearest millimeter. A few subsamples contained fewer than 50 fish, reflecting low abundance on the corresponding sampling date. Scale samples for age and growth analysis were collected from each fish in subsamples. Pumpkinseed scales were taken at the tip of the depressed left pectoral fin; golden shiner scales were taken above the lateral line dorsal to the tip of the depressed left pectoral fin.

Aging, scale measurement, and back-calculation.—Growth histories of individual fish in subsamples were determined by aging and back-calculation of lengths at previous ages from scales (Busacker et al. 1990; Francis 1990). Ten or more scales per fish were cleaned and mounted between glass slides; large, opaque scales were impressed on acetate slides. All scales on slides were viewed when ages were assigned to fish, and a single reader did all aging. Scales from 30 fish of each species were viewed by a second reader without knowledge of age assignments from the primary reader, and age assignments were in 100% agreement. Ages assigned by reading scales corresponded well with length-frequency distributions.

Anterior radii and interannular distances on 10 scales per fish were measured to the nearest 0.01 millimeter by using a dissecting microscope (25× magnification), drawing tube, and computerized digitizing tablet as described by Frie (1982). These radii are hereafter referred to as scale lengths. Regenerated or otherwise distorted scales were not measured, resulting in fewer than 10 replicate scales measured from some fish. Replicate measurements were then averaged for each fish, providing precise estimates of scale lengths for back-calculations (Newman and Weisberg 1987).

With the data on individual fish body lengths and mean scale lengths described above, we then back-calculated body lengths at previous ages using the three primary proportional back-calculation methods reviewed by Francis (1990) and examined the effect of using an alternative body-scale regression as advocated by Ricker (1992). Whereas all fish from subsamples were used in generating body-scale relationships, fish judged to be older than 7 years were omitted from back-calculations to avoid potential errors from incorrect aging of older fish. Scale edge increments from fish collected in spring were also omitted from back-calculations (see below). Because 6-

and 7-year-old fish were relatively few and often missing in subsamples, we restricted this evaluation of back-calculation methods to fish aged 1 through 5.

Back-calculation methods included the widely used Fraser-Lee formula,

$$L_i = c + (L_c - c) (S_i/S_c),$$

a formula reflecting a scale-proportional hypothesis (SPH) credited to Hile (1941),

$$L_i = -(a/b) + [L_c + (a/b)] (S_i/S_c),$$

and a formula reflecting a body-proportional hypothesis (BPH) credited to Whitney and Carlander (1956),

$$L_i = [(c + dS_i)/(c + dS_c)]L_c;$$

L_i = back-calculated fish body length at age i , L_c = fish body length at capture, S_i = mean scale length at annulus i , S_c = mean scale total length, c = intercept from the regression of body length on mean scale length, a = intercept from the regression of mean scale length on body length, b = slope from the regression of mean scale length on body length, and d = slope from the regression of body length on mean scale length. Alternative body-scale regressions, which supply the intercept or c parameter, were evaluated for the Fraser-Lee method only and included the widely used ordinary least-squares regression (OR) and geometric mean regression (GMR). Detailed descriptions of the formulae and rationale of these methods can be found in Francis (1990) and Ricker (1992).

Validation of back-calculated lengths.—As a standard for comparison among the different back-calculation methods, we used direct measurements of body length at annulus formation obtained from the spring collections in each lake. These collections were made when water temperatures averaged 13.6°C among lakes (range, 9.2–16.0°C) and new annuli were not yet evident on scales. Thus, the observed body lengths from these collections represent a known standard for comparing back-calculated body lengths of fish at corresponding ages. Statistical comparisons were limited to fish of the same cohort and age as recommended by Francis (1990). In other words, observed body lengths of fish of a given age sampled in the spring were compared with corresponding back-calculated body lengths from similar aged fish sampled in late summer. Accuracy of the different back-calculation methods was judged by how closely they matched known body lengths at time of annulus formation.

Statistical analyses.—Data were analyzed with linear regression, geometric mean regression, analysis of variance (ANOVA), and analysis of covariance (ANCOVA). Potential differences in body-scale relationships among lakes were evaluated for each species by subjecting body lengths to ANCOVA with mean scale length as the covariate. Similar ANCOVAs were run for each combination of species and lake to test for potential differences due to sampling period. Linear regressions of fish body length on mean scale length, mean scale length on body length, and geometric mean regressions of body length on mean scale length were performed on the entire data set for each species to generate pooled body-scale relationships.

Patterns of length at age differed widely among species and lakes, making single analyses combining the effects of lake, age, and back-calculation method unwieldy. Therefore, potential differences among back-calculation methods were evaluated separately for each combination of species and lake by using 2-way ANOVAs with interactions. These ANOVAs tested the effects of back-calculation method and age on back-calculated body lengths. The four back-calculation methods evaluated were Fraser-Lee with OR, Fraser-Lee with GMR, SPH, and BPH.

A similar approach was used in testing for differences between back-calculated and observed body lengths; separate 2-way ANOVAs with interactions were performed for each combination of species and lake. These ANOVAs tested the effects of length estimate type and age on body length estimates. The length estimate types evaluated were observed body lengths and Fraser-Lee (OR) back-calculations.

All analyses were performed on untransformed data according to the GLM and REG procedures of SAS (SAS Institute 1988). Significance tests had an alpha of 0.05.

Results

Body-Scale Relationships

Subsamples from the 10 lakes yielded 1,049 pumpkinseeds and 1,085 golden shiners for calculation of body-scale relationships. The ANCOVAs testing the effects of lake on body-scale relationships showed similar results for both species; interactions of lake \times mean scale length were significant (pumpkinseeds: $F = 20.03$, $P = 0.0001$; golden shiners: $F = 11.36$, $P = 0.0001$). These significant interactions, due in part to very large

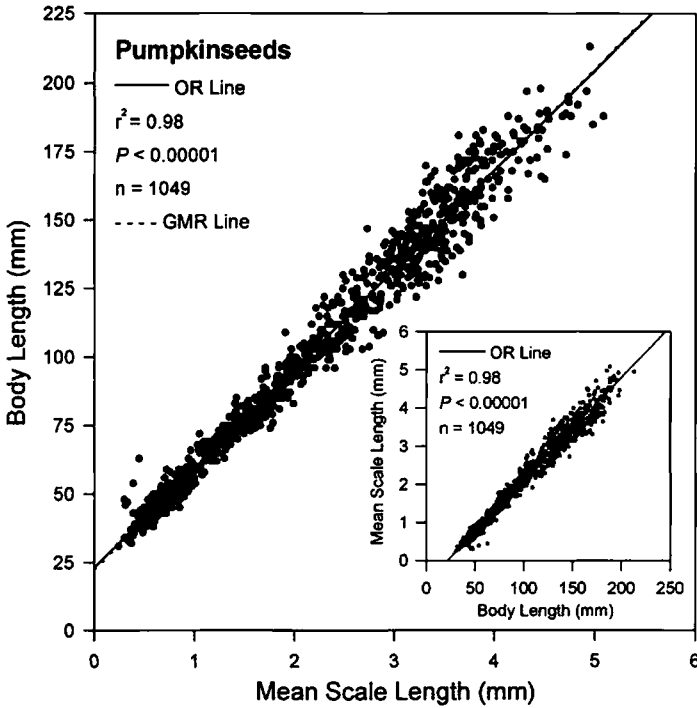


FIGURE 1.—Pumpkinseed body–scale relationships pooled from 10 southern Quebec lakes. Plotted points are body lengths and mean scale lengths of individual fish. Solid lines (OR) were generated by ordinary least-squares regression; dashed line (GMR) was generated by geometric mean regression. Regressions of body length on mean scale length (main graph) estimated parameters used for back-calculations based on the Fraser–Lee model and the body-proportional hypothesis. The regression of mean scale length on body length (inset graph) estimated parameters used for back-calculations based on the scale-proportional hypothesis.

sample sizes, imply slightly different trajectories for body–scale relationships among lakes. However, the tight fits of the pooled data in Figures 1 and 2 suggest that lake-specific regressions are unnecessary for characterizing the body–scale relationships for these two species. The average difference between lake-specific and pooled OR intercepts was 1.7 mm for pumpkinseeds and 4.9 mm for golden shiners.

The ANCOVAs testing the effects of sampling period on body–scale relationships also showed similar results for the two species. Nine of the 10 ANCOVAs for each species indicated no significant difference in body–scale relationship between the two sampling periods. The sampling period \times mean scale length interaction was significant ($F = 5.71$, $P = 0.019$) for Roxton Pond pumpkinseeds, indicating slightly different body–scale trajectories among sampling periods. The sampling period main effect was significant ($F = 4.73$, $P = 0.031$) for Roxton Pond golden shiners; body length averaged 2.6 mm greater for a given scale length in the spring than in late summer.

Because of the very minor differences among lake-specific regressions, the general lack of seasonal effects, and the excellent fit of the pooled regressions, pooled body–scale regressions were used to generate the intercepts (c parameter in Fraser–Lee, a parameter in SPH) and slopes (b parameter in SPH, d parameter in BPH) used in back-calculations. These pooled body–scale relationships were linear for both species and explained very high percentages of variance (Figures 1, 2).

For pumpkinseeds, the intercepts (c) generated by OR and GMR regression of body length on mean scale length were very similar, 23.2 and 22.3 respectively. Corresponding golden shiner OR and GMR intercepts, 19.1 and 16.6 respectively, were also similar but not quite as close as the pumpkinseed estimates. Slopes (d parameter used in BPH) generated by OR and GMR were also very similar, 36.3 versus 36.7 for pumpkinseeds and 49.8 versus 51.1 for golden shiners. The similarity of OR and GMR regressions for both species can be seen by the nearly superimposed lines in Figures 1 and 2.

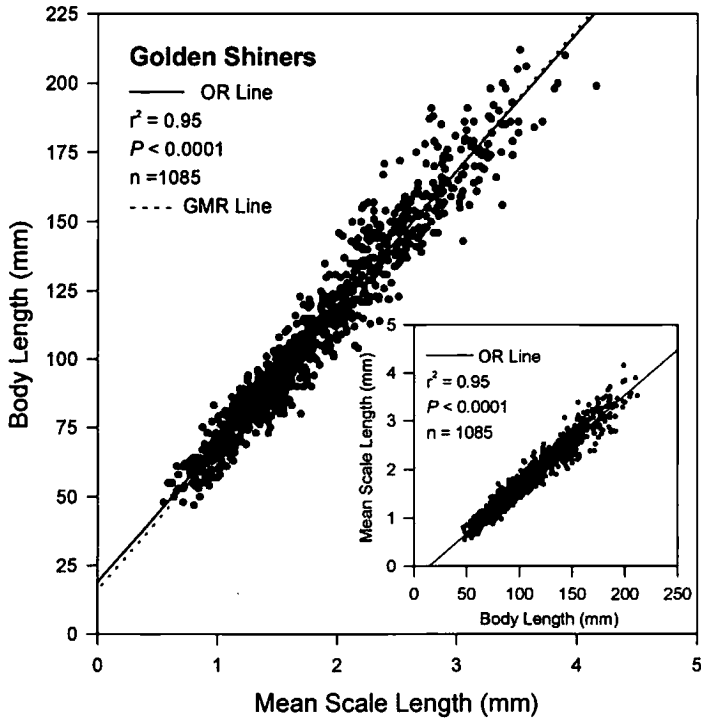


FIGURE 2.—Golden shiner body–scale relationships pooled from 10 southern Quebec lakes. Details are the same as those for Figure 1.

Comparisons among Back-Calculation Methods

Subsamples from the 10 lakes yielded 990 pumpkinseeds and 1,050 golden shiners, or roughly 100 fish per species per lake, for back-calculation of body length at previous ages. Omission of all fish greater than 5 years old and of 1-year-old fish from spring collections caused these totals to be slightly lower than those used in generating body–scale relationships. Mean body lengths estimated by the four back-calculation methods were very similar for both species and across the 5 age-classes and 10 lakes examined (Figures 3, 4). For an individual fish, differences among body lengths back-calculated by the four methods for a given age typically varied by 1 mm or less. These very small absolute differences among methods were not statistically significant in any of the 20 ANOVAs ($P \gg 0.05$ for both method main effect and method \times age interaction in all ANOVAs). For the two species and 10 lakes we studied, all four back-calculation methods gave essentially the same results.

Comparisons of Back-Calculated Lengths with Observed Lengths

Back-calculated body lengths corresponded well with observed body lengths in most cases, al-

though there were some exceptions (Figures 3, 4; Table 1). For pumpkinseeds, back-calculated and observed body lengths matched very closely in most lakes and age-classes; observed lengths averaged either slightly higher or lower than back-calculated lengths in a few cases. Only one pumpkinseed ANOVA indicated a significant effect of length estimate type (Table 1). In Lake Massawippi, observed lengths were greater than back-calculated lengths for age-1 pumpkinseeds, whereas back-calculated lengths were greater for older fish (Table 1; Figure 3).

Back-calculated and observed body lengths were somewhat more divergent in golden shiner populations, both in magnitude (Figure 4) and statistically (Table 1). Six of the 10 golden shiner ANOVAs indicated significant differences between back-calculated and observed lengths (Table 1). In four lakes—d'Argent, Hertel, Magog and Roxton Pond—observed lengths were greater than back-calculated lengths for young golden shiners, whereas back-calculated lengths were equal or greater than observed lengths for older fish (Table 1; Figure 4). Although not statistically significant, a similar pattern of interaction among length estimate type and age is suggested in the Lake Mem-

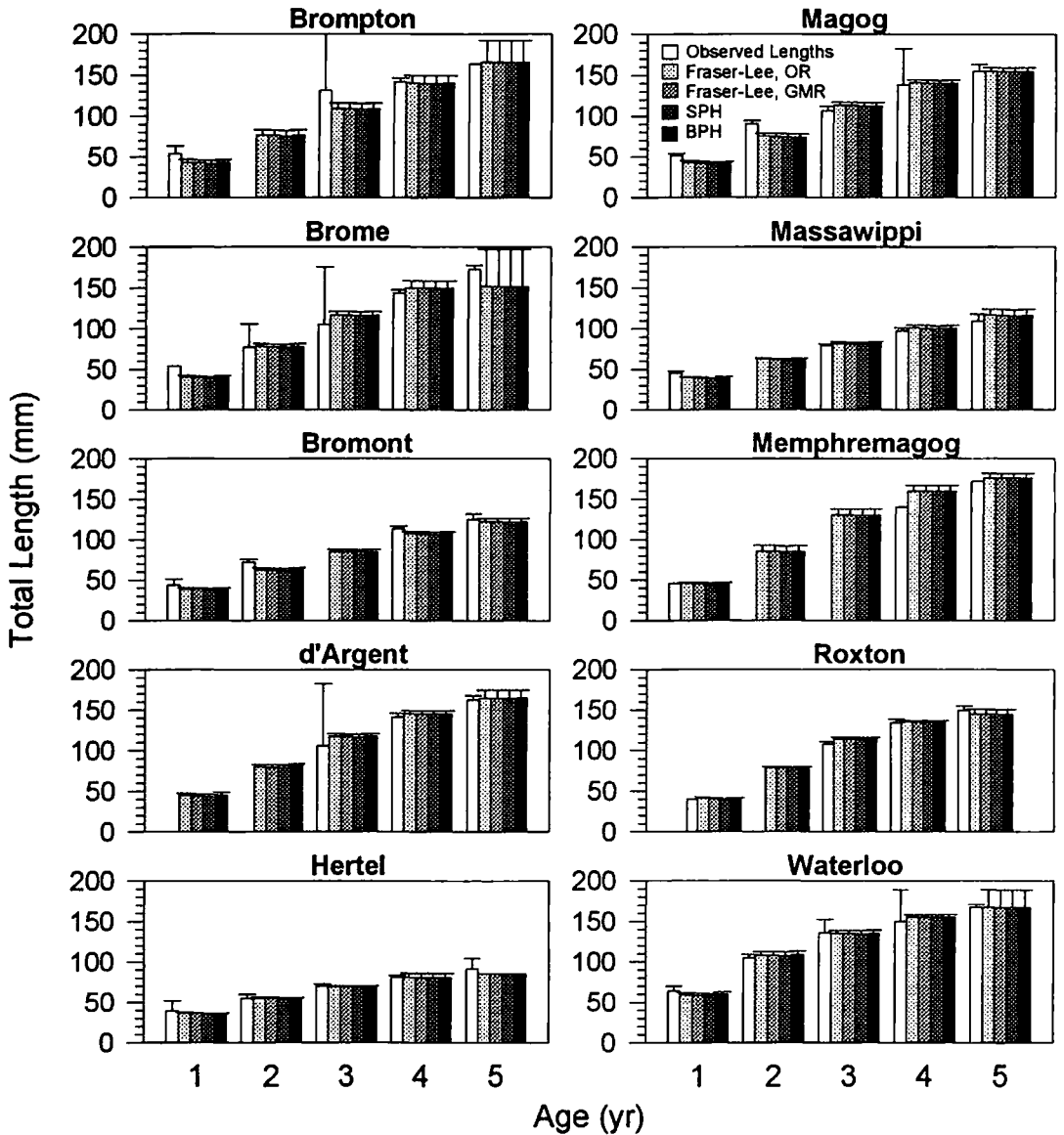


FIGURE 3.—Mean (+ half the 95% confidence interval) back-calculated and observed total lengths for pumpkinseeds aged 1–5 in 10 southern Quebec lakes. Back-calculated lengths (shaded bars) were generated by one of four methods. Observed lengths (open bars) were obtained from fish collected in the spring at time of annulus formation. Key is in the upper right panel.

phremagog golden shiner data (Figure 4). Observed lengths were consistently greater than back-calculated lengths in golden shiners from Lake Brome (Figure 4; Table 1).

Although differing in magnitude and occurring in different lakes, the differences between back-calculated and observed body lengths followed a similar age-related pattern in both species (Figure 5). Differences were greatest for 1-year-old fish,

averaging roughly 10% for pumpkinseeds and 25–30% for golden shiners. In nearly all cases where this difference was evident, observed lengths were greater than back-calculated lengths. For fish older than 1 year, differences were much lower and fairly consistent between the two species, averaging roughly 5%. The signs of these differences in older fish were more variable; observed lengths were less than or greater

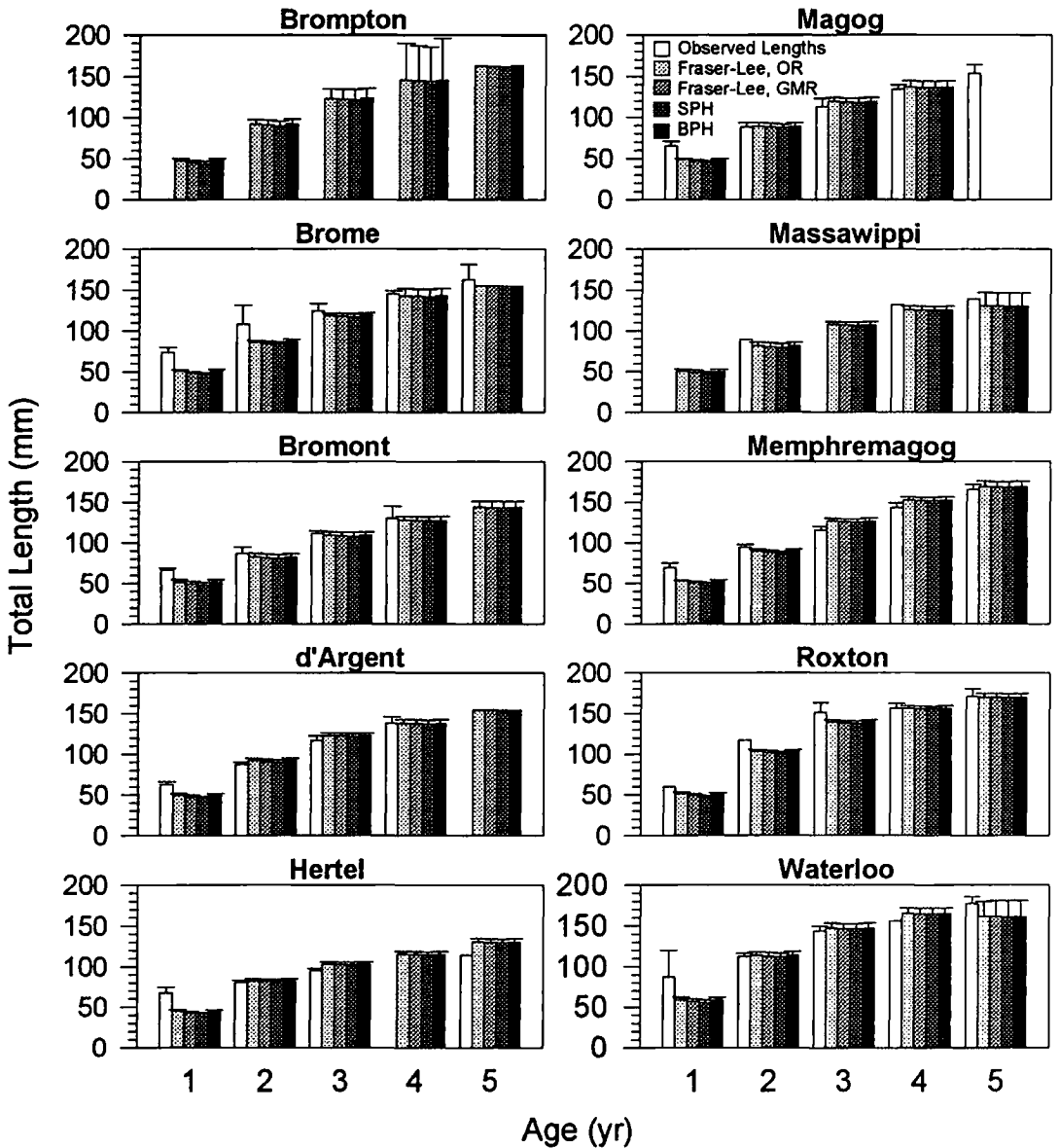


FIGURE 4.—Mean (+ half the 95% confidence interval) back-calculated and observed total lengths for golden shiners aged 1–5 in 10 southern Quebec lakes. Details are the same as those for Figure 3.

than back-calculated lengths with nearly equal frequency.

Discussion

Despite the importance and widespread use of back-calculation in studies of fish growth, there remains an abundance of different approaches in common use, considerable confusion surrounding certain methods, and little agreement on which method is best (Francis 1990; Ricker 1992; Schramm et al.

1992). In the most thorough review to date, Francis (1990) described in detail all the proportional methods and attempted to classify them theoretically based on hypotheses implied in their formulation. Francis (1990) concluded that the SPH and BPH methods are preferable to others because of their solid theoretical bases, and rejected the Fraser-Lee method because of its lack of a clear underlying hypothesis regarding the body-scale relationship. Francis also rejected use of GMR on

TABLE 1.—Summary of ANOVAs testing the effects of length estimate type and age on length estimates for pumpkinseeds and golden shiners in 10 southern Quebec lakes. Analysis of estimate type tested for differences between Fraser-Lee (ordinary regression) back-calculated lengths and observed lengths. Tabled values are *F*-ratios based on type III sums of squares (SAS Institute 1988). Asterisks indicate significant effects: $0.05 > P^* \geq 0.01$, $0.01 > P^{**} \geq 0.001$, $0.001 > P^{***} \geq 0.0001$, $0.0001 > P^{****}$.

Lake	Pumpkinseeds			Golden shiners		
	Type (T)	Age (A)	T × A	Type (T)	Age (A)	T × A
Brompton	1.49	104.85****	1.29		157.66****	
Brome	1.31	117.67****	0.22	37.10****	145.70****	1.38
Bromont	3.99	238.79****	0.11	0.14	81.93****	0.41
d'Argent	0.11	114.77****	2.01	0.95	258.24****	4.94**
Heriel	0.40	93.03****	0.40	1.13	160.27****	20.65****
Magog	1.33	399.13****	0.94	8.93**	154.66****	13.87***
Massawippi	4.24*	354.40****	4.50**	1.16	117.78****	0.03
Memphremagog	1.25	309.63****	0.90	7.88**	312.35****	2.60
Roxton Pond	0.18	187.54****	0.68	1.61	154.50****	2.90*
Waterloo	0.93	235.98****	1.40	0.24	81.84****	2.32

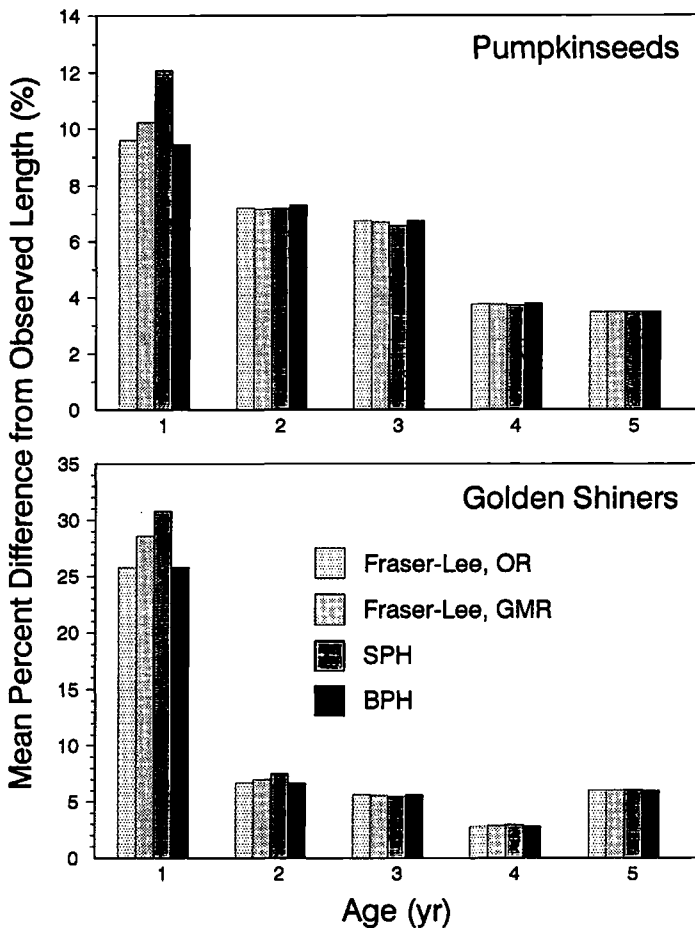


FIGURE 5.—Mean differences of back-calculated lengths from observed lengths of pumpkinseeds and golden shiners in 10 southern Quebec lakes, expressed as percentages of observed lengths. Back-calculated lengths were generated by one of four methods, indicated by shading (key is in the lower panel). Observed lengths were obtained from fish collected in the spring at time of annulus formation. Differences for individual fish were expressed as absolute values to avoid cancellation of positive and negative values.

theoretical grounds. Francis (1990) went on to lament the paucity of validation in back-calculation applications and used several published data sets to argue the point that using different back-calculation methods can result in large differences in estimated lengths. Ricker (1992) strongly supported the use of GMR and the Fraser-Lee method, both largely on theoretical grounds.

We believe our empirical results shed light upon two important questions regarding back-calculation. The first is, "Does back-calculation estimate growth history accurately?" Our comparisons of back-calculated body lengths with observed body lengths address this question and serve as a validation for the back-calculations. Secondly, "Which back-calculation method is best?" For the proportional methods that we evaluated, our comparisons tested for differences among back-calculation methods and for correspondence with observed body lengths. Previous synthetic reviews of back-calculation methods (Francis 1990; Ricker 1992) focused largely on theoretical analyses of various methods. Strengths and weaknesses inferred on theoretical grounds were then illustrated with data sets exhibiting much more variability (e.g., the mean r^2 for body-scale relationships in Francis' Table 2 is 0.83) than our data sets (Figures 1, 2). We do not dispute the theoretical conclusions of these reviews, nor do we contest the empirical evidence used to support them. However, we do question the source of high variability in these data sets in light of our finding of much tighter body-scale relationships for two species having different scale types and with data pooled across 10 lakes. Perhaps the older data sets were length-truncated or otherwise biased toward certain size-classes. Differences in true body-scale relationship variability among species are difficult to separate from potential variability introduced by sampling bias (Francis 1990; Ricker 1992) or errors in measuring both the fish (Gutreuter and Krzoska 1994) and scales (Hirschorn and Small 1987; Newman and Weisberg 1987) in different studies. We speculate that by obtaining a large and unbiased sample of the population, taking careful measurements of fish body length to the nearest millimeter, using currently available digitizing pad or video image analysis technology for accurately and precisely measuring scales to the nearest 0.01 millimeter, and averaging measurements from multiple scales, much better body-scale relationships could be obtained for most species than have been reported in the past. We further speculate that this level of detail would result in negligible differences among

back-calculation methods for other species, as we have demonstrated for pumpkinseeds and golden shiners.

Our results suggest that the Fraser-Lee, SPH, and BPH methods all give equivalent results when based on body-scale relationships that are linear and have high r^2 values. Furthermore, the choice of OR or GMR for generating body-scale relationships appears not to affect resulting estimates. Francis (1990) suggested back-calculating lengths by both SPH and BPH methods and interpreting the differences as rough estimates of back-calculation error. In our study, these differences were typically around 1 mm regardless of which methods were being compared. Given all the difficulties in obtaining unbiased samples and the relative imprecision inherent in many field measurements, we believe that this level of back-calculation error would be more than acceptable in most applications.

Although our back-calculated body lengths generally corresponded well with observed body lengths, there were several exceptions that raise questions about our method of validation. The most consistent disagreement was with age-1 fish, for which observed lengths were frequently greater than back-calculated lengths. This pattern closely resembles the well known "Lee's phenomenon" (Lee 1920), which is generally attributed to back-calculation error, differential mortality, biased sampling, or some combination thereof (Ricker 1969, 1992). We doubt that our discrepancies resulted from back-calculation error, because they did not occur in all lakes and they were more prominent for golden shiners than for pumpkinseeds. We suspect that the most likely cause of these discrepancies was either missing the appropriate spring sampling time of annulus formation for young fish in some lakes or biased sampling in the spring such that the smaller age-1 fish were underrepresented. Due to their fusiform bodies, the smallest age-1 golden shiners may have escaped through the 6-mm mesh of our seine. Alternatively, differential habitat use or other behavioral differences may have introduced unknown biases into our samples. Because of problems such as these, Francis (1990) recommended comparing back-calculated lengths with observed lengths for individual fish as the preferred method of validation, although conceding that this was far more difficult than validation based on comparisons among groups.

Despite these potential problems, our back-calculated body lengths typically differed from observed body lengths only by about 5% for fish older than age 1, indicating that back-calculation

reasonably estimates length at age for these species. Because this type of validation is far more practical than validation based on individual fish in most field populations, we suggest that it is a reasonable approach. However, we agree with Francis (1990) that obtaining unbiased samples is extremely important when this method is used, that timing of sampling for observed lengths is critical, and that interpretations must be made with caution.

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