

Accuracy and Precision of Estimates of Back-Calculated Channel Catfish Lengths and Growth Increments Using Pectoral Spines and Otoliths

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Abstract.—Back-calculation of lengths at previous ages using measurements of growth increments on the bony structures of fish is a common practice, yet studies validating this procedure are few. Our objective was to determine the accuracy and precision of back-calculated lengths and the last growth increment for channel catfish *Ictalurus punctatus* using pectoral spines and otoliths. In recent studies, the last growth increment has been related to the length of the fish at the start of the growing season to determine size-specific growth. Growth increments on basal sections of pectoral spines were measured along three radii—posterior (SP), anterior (SA), and lateral (SL)—and otoliths were measured along the ventral radius by three independent readers. Back-calculated lengths derived from eight models (biological intercept, body-proportional hypothesis [BPH] linear, BPH nonlinear, Dahl–Lee, Fraser–Lee, Morita–Matsuishi, scale-proportional hypothesis [SPH] linear, and SPH nonlinear) for each bony structure radius were compared with the actual growth histories of captive channel catfish to determine the best model and radius (for pectoral spines) for the two bony structures. The SPH linear model for SL provided the most accurate data for pectoral spines and was also appropriate for otoliths. Back-calculated lengths and last growth increments were considerably more accurate and precise for SL than for otoliths. The SPH linear model provided an initial length–last growth increment relationship that was similar to the observed relationship for SL but not for otoliths. We also estimated last growth increments and the initial length–last growth increment relationship from the traditionally used Dahl–Lee model for SP and found that these estimates were similar to those derived from the SPH linear model for SL. We recommend using the SPH linear model for SL to estimate length-at-age and growth increment data. However, the Dahl–Lee model for SP also provides reasonable estimates of the last growth increment.

Back-calculation of lengths at previous ages using measurements of growth increments on the bony structures of fish is a common practice (Francis 1990; Maceina et al. 2007). This technique provides estimates of the growth histories for individual fish, allowing for the estimation of length at ages at which fish are not vulnerable to capture, thereby increasing the sample size of length-at-age and growth increment data (Francis 1990; Schramm et al. 1992; Pierce et al. 1996). This technique, however, assumes that the growth in length is proportional to that on bony structures (Campana 1990; Francis 1990; Pierce et al. 1996). Considerable error in back-calculated lengths at previous ages can occur when the growth on bony structures is decoupled from somatic growth (Campana 1990). Despite this potential problem, relatively few studies have attempted to validate back-calculation procedures (Francis 1990; but see Klumb et al. 1999a, 1999b, 2001). Some studies have compared back-calculated mean lengths with the observed mean

lengths for that age-cohort in the population (e.g., Pierce et al. 1996); however, true validation requires that the actual growth histories of individual fish or groups of fish be compared with their own back-calculated lengths (Klumb et al. 1999a, 2001).

Growth increment–based back-calculations of length using basal sections of pectoral spines are commonly used for channel catfish *Ictalurus punctatus* (De Roth 1965; Elrod 1974; Eder and McDannold 1987; Gerhardt and Hubert 1991; Shrader et al. 2003). This technique has not been validated, although Marzolf (1955) identified a potential problem with the procedure. He demonstrated that basal sections are taken at progressively more distal locations as the pectoral spine grows. Changes in the sectioning location result in an increasing underestimation of length at the earliest ages. Growth increments are commonly measured along the posterior radius of the basal section where this bias occurs (Marzolf 1955). Marzolf (1955) suggested that measuring growth increments along the anterior rather than the posterior radius would reduce this bias. In response to these findings, De Roth (1965) sectioned spines at the same location regardless of spine size, but we are unaware of any studies

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evaluating growth measurements along the anterior radius, as Marzolf (1955) suggested.

Over the past couple of decades, otoliths have become the structure of choice for age estimation of many fish species (e.g., Boxrucker 1986; Hoxmeier et al. 2001; Long and Fisher 2001; Buckmeier and Howells 2003; Brown et al. 2004; Vandergoot et al. 2008), including catfish (Nash and Irwin 1999; Buckmeier et al. 2002; Maceina and Sammons 2006). Otoliths usually provide more accurate and precise estimates of age than other structures, such as scales and spines (Maceina et al. 2007). While back-calculation using otoliths has been done with other species (Boxrucker 1986; Schramm et al. 1992; Howells et al. 1997; Klumb et al. 2001), we found no studies that used this method with catfish. Some studies of other species have shown that the growth of otoliths is not proportional to that in fish length (Campana 1990; Barber and Jenkins 2001; Fey 2006). In particular, the otolith–fish length relationship can vary with fish growth rate, temperature, and food ration (Mosegaard et al. 1988; Reznick et al. 1989; Secor and Dean 1989; Barber and Jenkins 2001; Fey 2006). Validation studies with centrarchids revealed that back-calculated lengths typically overestimated the lengths at the youngest ages and underestimated those at the oldest ages (Howells et al. 1997; Klumb et al. 2001). Whether or not back-calculation using otoliths produces accurate length-at-age information for catfish is unknown.

In addition to providing length-at-age estimates, back-calculation provides estimates of growth increments. Biologists commonly attempt to relate the previous growth increments to various environmental variables. Recently, some studies have related the last growth increment to the length at the start of the growing season by means of linear regression for various fish species, including channel catfish, and then compared the size-specific estimates of growth from these regressions with the trends in environmental variables among systems (Putnam et al. 1995; Shoup et al. 2007; Michaletz 2009). Growth increments and initial lengths were estimated via back-calculation using pectoral spines for channel catfish. These studies assumed that the estimates of the last growth increment and the initial length based on back-calculation were reasonably accurate, but this has not been proven for channel catfish.

Because there is uncertainty about the validity of using pectoral spines and otoliths for back-calculating length at age and growth increments for channel catfish, we attempted to validate these procedures. Specifically, our objective was to determine the accuracy and precision of back-calculated lengths and the last growth increment for channel catfish using pectoral spines and otoliths. To accomplish this

objective, we first compared back-calculated lengths estimated from pectoral spines and otoliths using eight back-calculation models with actual growth histories of captive channel catfish. We then selected the best back-calculation model for each bony structure and compared the accuracy and precision of back-calculated lengths and growth increments between pectoral spines and otoliths. Our findings reveal substantial differences in back-calculation estimates among methods; consequently, we provide recommendations for future age and growth studies of channel catfish.

Methods

Captive fish.—Thirty age-0 channel catfish were initially reared on commercial food pellets in a hatchery pond during 2003, then tagged that October with Carlin dangler tags following the procedures in Wydoski and Emery (1983). Stainless steel wire was used to affix the uniquely numbered tag to the body of each fish just below the dorsal spine. Prior to tagging, each fish was measured for total length (TL; nearest 0.1 in). These fish were then held in a hatchery pond over the winter. The following April they were removed from the pond, measured, and placed in another hatchery pond until they were transferred to a 0.5-acre research pond in August 2004. In the research pond, the channel catfish were not artificially fed but rather preyed on the macroinvertebrates and green sunfish *Lepomis cyanellus* that inhabited the pond. Each fall and spring through 2008, the channel catfish were removed from the research pond, processed, and returned to the pond. Fish were captured by draining the pond down to the catch kettle and netting them. The pond was immediately refilled after fish were captured. During processing, each channel catfish was measured (TL) and its tag number was recorded. In addition, the left pectoral spine was removed from half of the fish and the right spine from the other half in fall 2006. If a fish was missing a tag, it was retagged.

Throughout the experiment, we were able to identify all untagged fish by a process of elimination using fish size or a combination of fish size and the absence of a left or right pectoral spine. Of the 30 fish, 17 retained their tags throughout the experiment, 11 had to be retagged once, and 2 had to be retagged twice. One fish died during the winter of 2007–2008, leaving only 29 fish at the end of the experiment. On October 31, 2008, fish were euthanized with an overdose of tricaine methanesulfonate (MS-222), measured for length, and had the remaining pectoral spine removed. Sagittal otoliths were then removed following the procedures outlined in Buckmeier et al. (2002), and gender was determined by examining gonads. The growth histories of individual fish were constructed from length

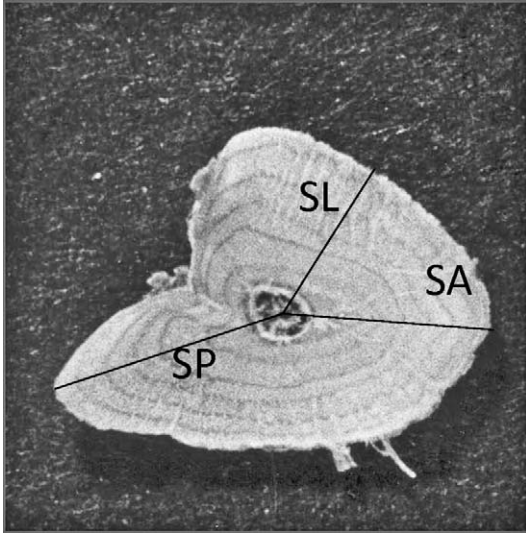


FIGURE 1.—Photograph of a basal section of a pectoral spine from a channel catfish indicating the radii along which growth increments were measured (SA = anterior, SL = lateral, and SP = posterior). Radius for SA = 0.11 in.

measurements made in April of each year and in October 2008. We chose to use April measurements instead of fall measurements (except for October 2008) because some growth occurred after fall sampling in years when sampling occurred in September or early October and fish collected in April had not put on new growth (a new annulus had not yet been formed).

Bony structures.—Pectoral spines were cleaned and softened before sectioning following standard procedures used by the Missouri Department of Conservation. First, the spines were placed in vials containing a warm, 7% solution of Biz laundry detergent; these vials were warmed for 16–18 h at 38°C in a drying oven. Then the detergent solution was removed from the vials and replaced with a cold, 50%-ammonia solution. After a minimum of 5 h, the ammonia solution was replaced with a cold, 50% solution of 95% ethyl alcohol. The spines were stored in the alcohol solution until they were sectioned with a Buehler Isomet low-speed saw. Several sections (0.35 mm thick) were taken from the articulating process and basal portions of each spine and placed in a coin envelope for later viewing.

Otoliths were processed following procedures modified from Buckmeier et al. (2002). The otoliths were burned by placing them on a hotplate, then mounted upright in thermoplastic cement on a microscope slide and sanded until the nucleus was revealed. Because we had difficulty measuring growth increments, we further processed the otoliths by reheating the cement, reattaching the otolith with the sanded side down, allowing the

cement to reharder, and then sanding the other side of the otolith until the nucleus was revealed. This additional sanding made the annuli more distinct, enabling us to more accurately measure the growth increments.

The pectoral spine and otolith sections were examined under a dissecting microscope, and the growth increments were measured by three independent readers on a projected image of these structures using a computer-aided digitizing program. All readers had prior fish age estimation experience, but none had previously examined channel catfish otoliths. The basal spine sections were viewed at 45× magnification using either side or transmitted illumination. Measurements were taken along three radii: posterior (SP), anterior (SA), and lateral (SL) (Figure 1). We wanted to determine whether SA was more accurate than SP, as suggested by Marzolf (1955). We also included SL to determine whether this radius provided more accurate length-at-age information. The otoliths were viewed at 90× magnification after their exposed surfaces were coated with glycerin. Growth increments were measured along the longest radius possible (usually the ventral radius) using side illumination (Buckmeier et al. 2002). Owing to the difficulty in viewing the annuli, it was not possible to measure all otoliths along the same radius. For most fish, both otoliths were available for viewing but only one (the easiest to view) was used for measurements.

Back-calculation models.—To determine the appropriate back-calculation model for each bony structure, back-calculated lengths from eight models were compared with the actual lengths at each age using bony structure measurements collected at the end of the experiment in 2008. To simplify the analysis, only the measurements made by reader 1 were used for the initial model comparisons. Once a model was selected for each structure, the data from all three readers were used to compare the accuracy and precision of the models for pectoral spines (2006 and 2008) and otoliths (2006).

Most of the back-calculation models required coefficients from regressions of bony structure radius and fish length (reviewed by Francis 1990 and Morita and Matsuishi 2001). The following equations were used to provide these coefficients:

$$B = a + bL \tag{1}$$

$$L = c + dB \tag{2}$$

$$B = uL^v \text{ or } \log_e B = \log_e u + v \cdot \log_e L \tag{3}$$

$$L = wB^k \text{ or } \log_e L = \log_e w + k \cdot \log_e B \tag{4}$$

$$B = \alpha + \beta L + \gamma t, \tag{5}$$

where B is the radius of the bony structure, L is the length of the fish, $a, b, c, d, u, v, w, k, \alpha, \beta,$ and γ are coefficients derived from the regression equations, and t is the age of the fish. One or more of these coefficients are used in the back-calculation models described below. The regressions were computed using known fish lengths at each age (age 1 to age at capture), the associated bony structure measurements at each annular mark, and the entire radius at time of capture.

The following eight back-calculation models were used (reviewed by Francis 1990 and Morita and Matsuishi 2001):

Dahl–Lee model:

$$L_t = L_T \left(\frac{B_t}{B_T} \right) \quad (6)$$

Scale-proportional hypothesis (SPH) linear model:

$$L_t = -\frac{a}{b} + \left(L_T + \frac{a}{b} \right) \frac{B_t}{B_T} \quad (7)$$

SPH nonlinear model:

$$L_t = \left(\frac{B_t}{B_T} \right)^{1/v} L_T \quad (8)$$

Body-proportional hypothesis (BPH) linear model:

$$L_t = \frac{c + dB_t}{c + dB_T} L_T \quad (9)$$

BPH nonlinear model:

$$L_t = \left(\frac{B_t}{B_T} \right)^k L_T \quad (10)$$

Fraser–Lee model:

$$L_t = c + (L_T - c) \left(\frac{B_t}{B_T} \right) \quad (11)$$

Morita–Matsuishi model:

$$L_t = -\frac{\alpha}{\beta} + \left(L_T + \frac{\alpha}{\beta} + \frac{\gamma}{\beta} T \right) \frac{B_t}{B_T} - \frac{\gamma}{\beta} t \quad (12)$$

Biological intercept model:

$$L_t = L_T + \frac{B_t - B_T}{B_T - B_0} (L_T - L_0). \quad (13)$$

In equations (6)–(13), L_t is the back-calculated length at age t , L_T is the length at the time of capture T , B_t is the radius of the bony structure at annulus t , and B_T is the radius of the bony structure at T . In equation (13), B_0 is the observed initial bony structure radius and L_0 is the initial fish body length. For our channel catfish, B_0 was assumed to be 0.0004 in for otoliths

(Sakaris and Irwin 2008), 0.0028 in for SA, 0.0016 in for SL, and 0.0019 in for SP (approximated from measurements on larvae; unpublished data), and L_0 was assumed to be 0.3 in (Auer 1982).

To determine the most appropriate back-calculation model for pectoral spines and otoliths, the observed lengths were compared with those predicted by the models through linear regression, as in Morita and Matsuishi (2001) except that the observed length was the dependent variable in accordance with Piñeiro et al. (2008). We determined whether the intercept of the regression equation differed ($P \leq 0.05$) from 0 and the slope from 1 using t -tests. We assumed that the best model was the one that most closely matched the 1:1 line between predicted and observed data and explained a large amount of the variance in the relationship. To further determine the relative accuracy of the best model for each bony structure, we computed the percent error of back-calculated length estimates, namely,

$$\frac{L_b - L_o}{L_o} \times 100, \quad (14)$$

where L_b is the back-calculated length and L_o is the observed length. We also computed percent error based on absolute values to avoid the cancellation of positive and negative values when means were computed (Mayer and Butler 1993). To determine precision, we calculated the coefficient of variation (CV [$100 \cdot \text{SD}/\text{mean}$]) of the back-calculated length estimates among the three readers for each individual fish and then averaged these values over all fish. We also computed the CV between back-calculated lengths estimated from pectoral spines collected in 2006 and 2008 for individual fish and averaged these values to determine whether the length estimates for fish at young ages changed over time.

The last growth increments were compared in the same way as the back-calculated lengths. However, these increments were only computed using the best back-calculation model for each bony structure and the Dahl–Lee model for SP. We included the Dahl–Lee model for SP because it has previously been used to compute the last growth increment (Putnam et al. 1995; Shoup et al. 2007; Michaletz 2009) and we wanted to determine whether this model provided a valid estimate. Growth increments were estimated for 2006 by subtracting the back-calculated lengths at age 3 from the observed lengths for fall 2006, using measurements from pectoral spines collected that fall. These estimates were compared with the observed growth increments computed by subtracting the observed lengths in spring 2006 from those in fall 2006. Estimates could only be made from pectoral

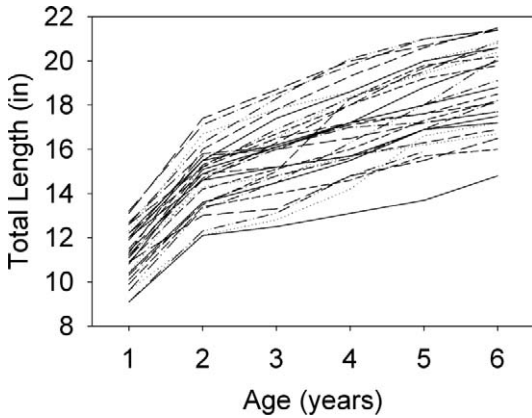


FIGURE 2.—Growth histories of individual channel catfish used in the study.

spine measurements for 2006 because otoliths were not collected that year. Similar methods were used to derive the estimated and observed growth increments for 2008 except that estimates were computed from both pectoral spine and otolith measurements. Linear regression, percent error, absolute percent error, and CV among readers were computed following the methods described for back-calculated length data.

We determined whether errors in the estimation of lengths and growth increments would affect the relationship between the last growth increment and the length of the fish at the start of the growing season that was used by Putnam et al. (1995), Shoup et al. (2007), and Michaletz (2009) to determine size-specific growth. A two-way analysis of covariance (ANCOVA) was used to determine how initial length (the covariate) and method (observed versus bony structure and back-calculation model) affected growth increments. A separate ANCOVA was conducted for each reader for both the 2006 and 2008 growth increment data.

Results

Channel catfish exhibited highly variable growth among individuals (Figure 2). At the end of six growing seasons, they ranged in length from 14.8 to 21.5 in with a mean length of 18.9 in. With few exceptions, fish that were small at age 1 remained small and fish that were large at age 1 remained large (relative to other fish) throughout the experiment. Of the 29 fish that survived to fall 2008, 22 were males and 7 were females. The males grew faster than the females. Length at age 1 did not differ significantly between genders (analysis of variance: $F = 0.43$; $df = 1, 27$; $P = 0.52$), but by the end of the experiment males were significantly larger than females ($F = 6.26$;

TABLE 1.—Regression equations relating bony structure radius (B), fish body length (L), and fish age (t [years]). Bony structures are the anterior radii (SA), lateral radii (SL), and posterior radii (SP) of pectoral spines and otoliths. Models are based on 2008 data from reader 1. Sample sizes are 174 for pectoral spines and 138 for otoliths.

| Model | r^2 or R^2 | P |
|-------------------------------------|----------------|---------|
| SA | | |
| $B = 0.004 + 0.006L$ | 0.783 | <0.0001 |
| $L = 2.968 + 133.546B$ | 0.783 | <0.0001 |
| $\log_e B = -5.101 + 0.999\log_e L$ | 0.807 | <0.0001 |
| $\log_e L = 4.653 + 0.808\log_e B$ | 0.807 | <0.0001 |
| $B = 0.017 + 0.004L + 0.003t$ | 0.811 | <0.0001 |
| SL | | |
| $B = -0.022 + 0.006L$ | 0.886 | <0.0001 |
| $L = 5.129 + 147.959B$ | 0.886 | <0.0001 |
| $\log_e B = -6.283 + 1.320\log_e L$ | 0.900 | <0.0001 |
| $\log_e L = 4.559 + 0.682\log_e B$ | 0.900 | <0.0001 |
| $B = -0.022 + 0.006L + 0.0001t$ | 0.886 | <0.0001 |
| SP | | |
| $B = -0.017 + 0.008L$ | 0.728 | <0.0001 |
| $L = 5.824 + 86.652B$ | 0.728 | <0.0001 |
| $\log_e B = -5.837 + 1.327\log_e L$ | 0.743 | <0.0001 |
| $\log_e L = 3.976 + 0.560\log_e B$ | 0.743 | <0.0001 |
| $B = 0.009 + 0.005L + 0.007t$ | 0.780 | <0.0001 |
| Otoliths | | |
| $B = -0.006 + 0.004L$ | 0.334 | <0.0001 |
| $L = 11.336 + 89.206B$ | 0.334 | <0.0001 |
| $\log_e B = -6.095 + 1.127\log_e L$ | 0.324 | <0.0001 |
| $\log_e L = 3.622 + 0.287\log_e B$ | 0.324 | <0.0001 |
| $B = 0.007 + 0.002L + 0.003t$ | 0.364 | <0.0001 |

$df = 1, 27$; $P = 0.02$; male TL = 19.4 in, female TL = 17.5 in).

Bony Structure Radius and Body Length Relationships

Bony structure radius and body length were significantly related (all $P < 0.0001$) for all bony structure radii based on 2008 data for reader 1 (Table 1). However, the relationships for SL explained the most variation (all $r^2 > 0.88$) and those for otoliths the least (all $r^2 < 0.37$). When age (t) was incorporated into the equations (which is needed for the Morita–Matsuishi model), the r^2 values increased by less than 6% over those for the models with only body length. The sample size was lower for otoliths than for pectoral spines because otoliths were successfully removed from only 23 fish. The bony structure radius–body length relationships for readers 2 and 3 for 2008 data and for all readers for 2006 data were nearly identical to those shown in Table 1 and are not reported here.

Back-Calculated Lengths

When the 2008 data for reader 1 were used, both the back-calculation model and bony structure radius affected the accuracy of the back-calculated lengths. For all models and radii, back-calculated lengths were

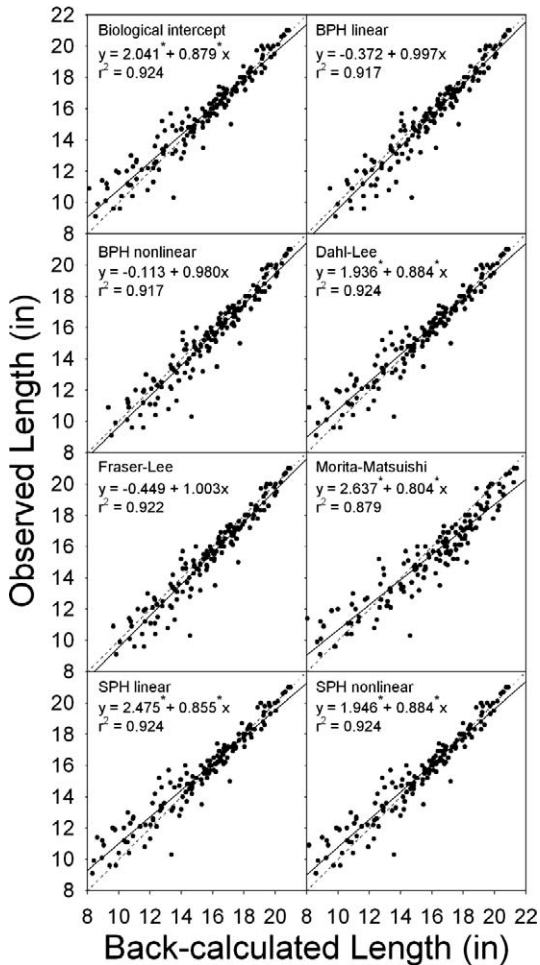


FIGURE 3.—Relationships between observed and back-calculated lengths using the biological intercept, body-proportional hypothesis (BPH) linear, BPH nonlinear, Dahl-Lee, Fraser-Lee, Morita-Matsuishi, scale-proportional hypothesis (SPH) linear, and SPH nonlinear models based on anterior radii measurements of pectoral spines made by reader 1 for 2008 data. The dotted lines indicate 1:1 relationships and the solid lines the fitted regressions. Asterisks denote significant ($P \leq 0.05$) differences of the intercepts from 0 and the slopes from 1.

more accurate for older (larger) fish (Figures 3–6). For pectoral spines, models for SL (Figure 4) provided better fits (higher r^2 values) than models for SA (Figure 3) and SP (Figure 5). In particular, the SPH linear, SPH nonlinear, and Morita-Matsuishi models provided data that did not differ from the 1:1 relationship between observed and predicted lengths and had r^2 values that exceeded 0.96. We selected the SPH linear model as the best model for pectoral spines because it was simpler than the other two models but produced nearly

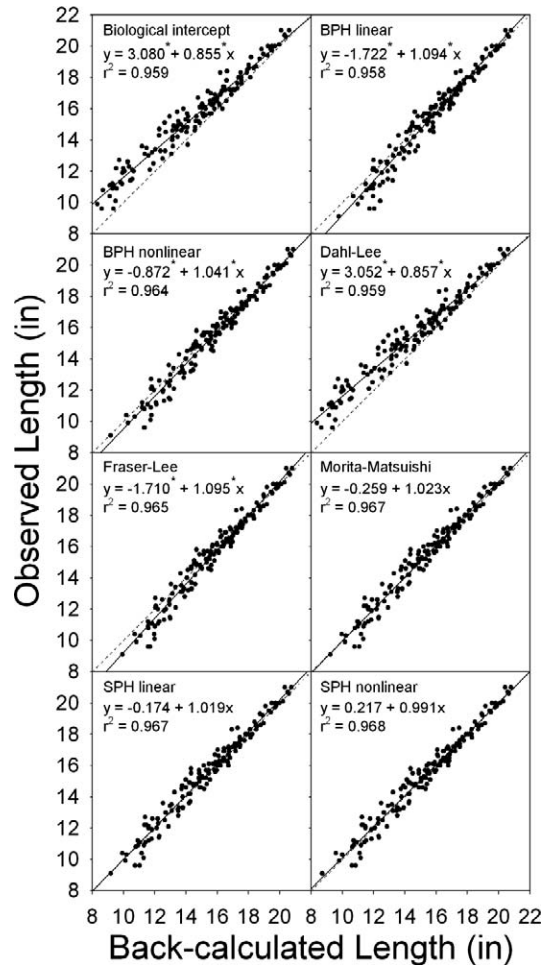


FIGURE 4.—Relationships between observed and back-calculated lengths using eight models based on lateral radii measurements of pectoral spines made by reader 1 for 2008 data. See Figure 3 for additional details.

identical results. For otoliths, none of the models provided data that closely fit the 1:1 relationship between observed and predicted lengths and model fits were poorer than those for pectoral spines (Figure 6). Only the BPH nonlinear model provided data that did not differ from the 1:1 line. However, this lack of difference was due to the broad scatter in the data, and this model consistently overestimated the observed lengths. We chose the SPH linear model for otoliths because it fit the data as well as or better than the other models and we had selected this model for pectoral spines.

Back-calculated lengths were more accurate and precise for SPH linear models for SL than for otoliths. On average, the SPH linear models underestimated

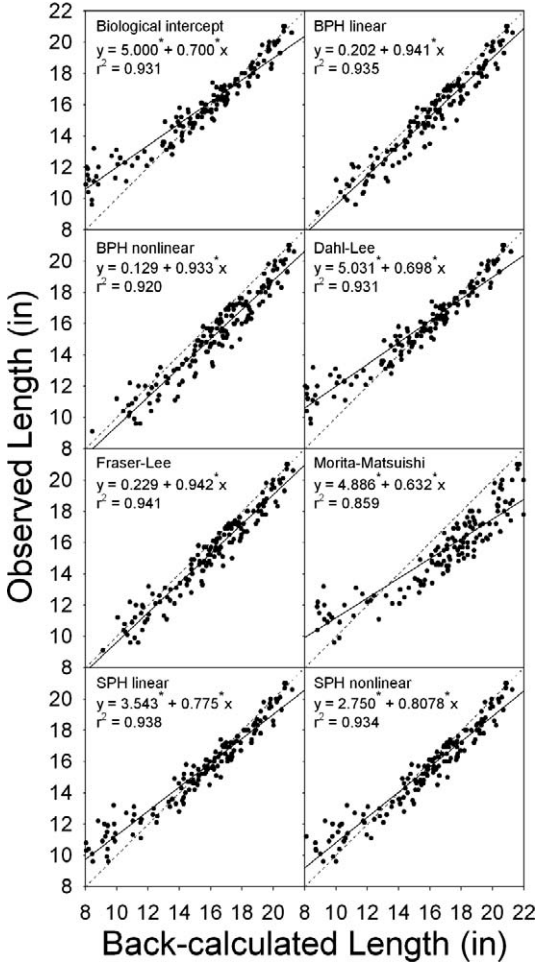


FIGURE 5.—Relationships between observed and back-calculated lengths using eight models based on posterior radii measurements of pectoral spines made by reader 1 for 2008 data. See Figure 3 for additional details.

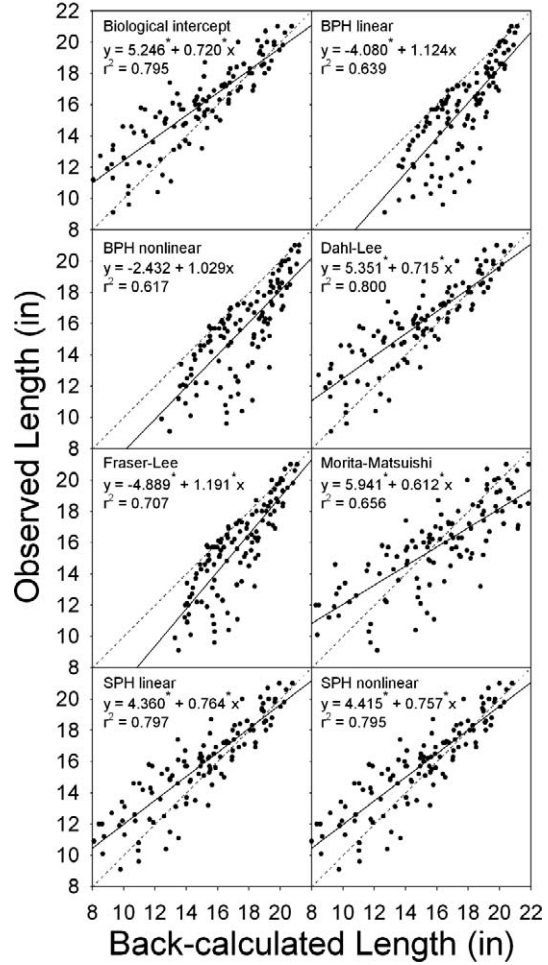


FIGURE 6.—Relationships between observed and back-calculated lengths using eight models based on ventral radii measurements of otoliths made by reader 1 for 2008 data. See Figure 3 for additional details.

lengths at age for both SL and otoliths, but these underestimates were less than 4% for SL but 5.9% or more for otoliths (Table 2). The absolute percent errors were also greater for otoliths (9.5–11.6%) than for SL (2.8–4.5%). Precision was higher for SL than for otoliths, the mean CV among readers being 2.6% or less for SL and 6.6% for otoliths. For SL, estimates of length for ages 1–3 were very similar using spines collected in 2006 and spines collected from the same fish in 2008. The mean CVs between 2006 and 2008 data were 2.4% (range, 0.03–11.7%) for reader 1, 2.9% (0.02–9.1%) for reader 2, and 2.6% (0.03–9.5%) for reader 3, indicating that the estimates of lengths did not substantially change as the fish became older.

Growth Increments

Estimates of the last growth increment derived from the back-calculation models were less accurate and precise than the back-calculated lengths. While the growth increments estimated from SPH linear models for SL and Dahl–Lee models for SP did not differ from the 1:1 relationship between observed and predicted data, the r^2 values were typically less than 0.60 (Table 3; Figure 7). The r^2 values were usually higher for the SPH linear model for SL than for the Dahl–Lee model for SP. Estimates of the last growth increment derived from SPH linear models for otoliths significantly varied from the 1:1 relationship for all readers (Table 3; Figure 7). The last growth increment was typically overestimated by all methods, but the two pectoral

TABLE 2.—Mean \pm SE percent error (PE) and absolute percent error (APE) for each of three readers and among-reader mean CVs for back-calculated lengths and last growth increments. Methods involve using pectoral spine–lateral radii and the scale-proportional hypothesis linear model (SL–SPH), pectoral spine–posterior radii and the Dahl–Lee model (SP–DL), and otoliths and the SPH linear method (OT–SPH) (see text for details). Only growth increments were computed using the SP–DL method.

| Year | Method | Reader 1 | | Reader 2 | | Reader 3 | | CV(range) |
|--------------------------|--------|-----------------|------------------|------------------|------------------|------------------|------------------|-----------------|
| | | PE | APE | PE | APE | PE | APE | |
| Lengths | | | | | | | | |
| 2006 | SL–SPH | -1.4 ± 0.5 | 3.4 ± 0.3 | -3.1 ± 0.5 | 4.5 ± 0.3 | -1.2 ± 0.5 | 3.9 ± 0.3 | 2.6 (0.2–8.0) |
| 2008 | SL–SPH | -0.6 ± 0.3 | 2.8 ± 0.2 | -0.7 ± 0.4 | 3.2 ± 0.2 | -1.7 ± 0.3 | 3.1 ± 0.2 | 1.9 (0.1–8.1) |
| | OT–SPH | -5.9 ± 1.0 | 9.5 ± 0.8 | -10.2 ± 0.9 | 11.1 ± 0.8 | -9.3 ± 1.0 | 11.6 ± 0.8 | 6.6 (0.4–24.7) |
| Growth increments | | | | | | | | |
| 2006 | SL–SPH | 4.0 ± 4.7 | 20.1 ± 3.0 | 28.4 ± 6.3 | 35.8 ± 4.9 | 3.4 ± 4.9 | 23.1 ± 2.3 | 18.9 (3.2–38.0) |
| | SP–DL | 22.8 ± 7.1 | 35.2 ± 5.1 | 29.3 ± 8.5 | 40.5 ± 6.8 | -5.5 ± 4.7 | 21.3 ± 2.7 | 21.2 (6.7–47.3) |
| 2008 | SL–SPH | 41.6 ± 11.4 | 51.3 ± 9.9 | 55.0 ± 12.9 | 60.8 ± 11.9 | 48.8 ± 11.4 | 56.3 ± 10.1 | 17.0 (1.2–49.1) |
| | SP–DL | 8.0 ± 8.2 | 32.1 ± 5.8 | 61.7 ± 13.9 | 70.6 ± 12.3 | 30.0 ± 9.7 | 42.4 ± 7.9 | 26.0 (3.9–51.0) |
| | OT–SPH | 82.3 ± 22.9 | 101.1 ± 19.2 | 183.0 ± 36.6 | 184.9 ± 36.1 | 136.7 ± 26.2 | 141.8 ± 24.9 | 29.8 (4.7–59.3) |

spine models provided more accurate estimates than the otolith model (Table 2). Absolute percent errors exceeded 100% for all readers for otoliths but were always less than 71% for pectoral spines. Of the two pectoral spine models, neither consistently provided the lowest absolute percent error among years and readers. Precision among readers was fairly consistent among models, the mean CV being somewhat lower for the SPH linear model for SL and higher for the SPH linear model for otoliths.

Initial Length–Growth Increment Relations

The initial length–last growth increment relationship differed among back-calculation methods for the 2008 ANCOVA models but not for the 2006 models (Table 4). The two pectoral spine models provided data similar to the observed relationship for the 2006 models. For the 2008 models, the relationship provided by the otolith model was significantly different from the observed relationship for all three readers. With one exception, the relationships derived from the two pectoral spine models were similar to the observed relationship for all readers for 2008. Length and the

interaction between length and method were not significant in any of the ANCOVA models.

Discussion

To our knowledge, this was the first attempt to validate back-calculation methods using pectoral spines and otoliths for channel catfish. We found substantial differences in accuracy among the combinations of bony structure radii and back-calculation models. The biases in back-calculated lengths decreased with increasing fish age (length) for all methods because length estimates were forced to approach the actual lengths at capture. Overall, the SPH linear model was the most appropriate for both pectoral spines (SL) and otoliths. Lateral radii measurements using the SPH linear model provided more accurate length information than either the traditional SP measurements or the SA measurements recommended by Marzolf (1955). However, both the SPH linear model for SL and the commonly-used Dahl–Lee model for SP provided similar estimates of the last growth increment that did not differ from the observed values. Back-calculated length and last growth increment data derived from the

TABLE 3.—Regression equations for observed growth increments (in, dependent variable) versus back-calculated growth increments (independent variable). Methods are as noted in Table 2. Asterisks denote significant ($P \leq 0.05$) differences of the intercepts from 0 and the slopes from 1. See Figure 7 for scatterplots and regression lines.

| Method | Reader 1 | | | Reader 2 | | | Reader 3 | | |
|-------------|-----------|---------|-------|-----------|---------|-------|-----------|--------|-------|
| | Intercept | Slope | r^2 | Intercept | Slope | r^2 | Intercept | Slope | r^2 |
| 2006 | | | | | | | | | |
| SL–SPH | 0.242 | 0.788 | 0.574 | 0.120 | 0.741 | 0.496 | 0.135 | 0.899 | 0.626 |
| SP–DL | 0.187 | 0.759 | 0.192 | 0.452 | 0.537 | 0.138 | 0.154 | 0.984 | 0.367 |
| 2008 | | | | | | | | | |
| SL–SPH | 0.055 | 0.758 | 0.489 | -0.098 | 0.799 | 0.650 | -0.017 | 0.790 | 0.583 |
| SP–DL | 0.112 | 0.911 | 0.532 | 0.176 | 0.574 | 0.156 | -0.020 | 0.904 | 0.350 |
| OT–SPH | 0.912* | -0.107* | 0.011 | 1.134* | -0.201* | 0.036 | 0.670 | 0.081* | 0.006 |

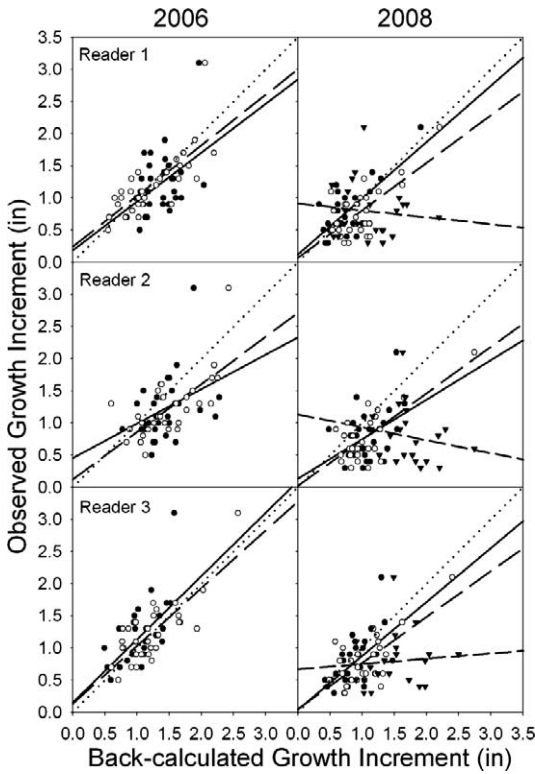


FIGURE 7.—Relationships between observed and back-calculated last growth increments using the Dahl–Lee model for posterior radii measurements on pectoral spines (solid circles and solid lines), the scale-proportional hypothesis (SPH) linear model for lateral radii measurements on pectoral spines (open circles and long-dashed lines), and the SPH linear model for ventral radii measurements on otoliths (inverted triangles and medium-dashed lines) made by the three readers for 2006 and 2008 data. Otolith data were not available for 2006. Dotted lines indicate 1:1 relationships. See Table 3 for regression parameters.

SPH linear model for SL were considerably more accurate and precise than those for otoliths.

The inaccuracy and imprecision of otolith-derived data may have been the result of several factors. First, although we could see the appropriate number of annuli when viewing the whole section of the otolith, not all annuli were always visible along the ventral radius. Thus, our measurements were not taken along the same radius for each otolith. This may have caused some of the variability in the measurements among readers. However, Klumb et al. (2001) found no consistent differences in the accuracy of back-calculated lengths for measurements taken along three radii on otoliths of bluegill *Lepomis macrochirus* × green sunfish hybrids. Second, many channel catfish otoliths had rather large opaque and elongated nuclei, making it

difficult to determine the center of the nucleus and properly measure growth increments. Finally, the growth of otoliths may not accurately reflect somatic growth. Many studies have shown that otolith growth is often decoupled from the growth in length owing to various factors, such as the fish’s growth rate, water temperature, and food ration (Mosegaard et al. 1988; Reznick et al. 1989; Secor and Dean 1989; Barber and Jenkins 2001; Fey 2006). Campana (1990) suggested using a biological-intercept procedure to correct for back-calculation bias for otoliths. However, making these slight adjustments had little effect on our results, as found by Klumb et al. (2001) for bluegill × green sunfish hybrids.

The errors were much larger for the last growth increment data than for the length data for SPH linear models for both SL and otoliths owing to a difference in scale. For example, underestimating the length of a 16-in fish by 0.2 in would only result in a percentage error of -1.25% . Conversely, underestimating an actual growth increment of 1 in by 0.2 in would result in a percentage error of -20% . Thus, small errors in estimating back-calculated lengths can result in rather large errors in estimating the last growth increment.

Back-calculation produces errors in the estimates of both the length at the start of the growing season and the last growth increment. These errors can affect the initial length–last growth increment relationship that was used by Putnam et al. (1995), Shoup et al. (2007), and Michaletz (2009) to determine size-specific growth. Fortunately, our data indicate that both the SPH model for SL and the previously-used Dahl–Lee model for SP can be used to estimate this relationship. Using back-calculation to estimate only the length at the last annulus and the last growth increment avoids the problem of increasing bias in estimating length at progressively younger ages (Gutreuter 1987; this study). The initial length–last growth increment relationship may be more useful than mean length-at-age data for determining growth rates because growth is more closely related to size than to age (Gerking and Rausch 1979; Gutreuter 1987). Interestingly, initial length was not significant in any of the ANCOVA models in this study. In contrast, growth increments were significantly related to initial length in most of the systems studied by Putnam et al. (1995), Shoup et al. (2007), and Michaletz (2009). Perhaps the lack of an initial-length effect in our study was a result of having only one age-class—with a narrower length range than would be observed in a population with multiple year-classes.

It is tempting to use back-calculation to determine lengths at young ages in order to separate hatchery-reared fish from naturally produced fish in systems that

TABLE 4.—Results of two-way ANCOVAs for the effect of initial total length (the covariate) and method (OB = observed; other abbreviations are as noted in Table 2) on growth increments. Otoliths were not available for 2006 analyses. No interactions were significant. For significant models ($P \leq 0.05$), post hoc comparisons among methods were made using Tukey–Kramer adjustments for multiple comparisons; methods without letters in common are significantly different.

| Reader | Factor | df | F | P | Method | | | |
|-------------|--------|-------|-------|---------|--------|--------|-------|--------|
| | | | | | OB | SL–SPH | SP–DL | OT–SPH |
| 2006 | | | | | | | | |
| 1 | Model | 3, 86 | 0.69 | 0.56 | | | | |
| | Length | 1, 86 | 0.20 | 0.66 | | | | |
| | Method | 2, 86 | 0.96 | 0.39 | z | z | z | |
| 2 | Model | 3, 86 | 2.41 | 0.07 | | | | |
| | Length | 1, 86 | 1.24 | 0.27 | | | | |
| | Method | 2, 86 | 3.18 | 0.05 | z | z | z | |
| 3 | Model | 3, 86 | 1.36 | 0.26 | | | | |
| | Length | 1, 86 | 2.08 | 0.15 | | | | |
| | Method | 2, 86 | 1.08 | 0.35 | z | z | z | |
| 2008 | | | | | | | | |
| 1 | Model | 4, 87 | 3.44 | 0.01 | | | | |
| | Length | 1, 87 | 0.34 | 0.56 | | | | |
| | Method | 3, 87 | 4.55 | 0.005 | z | zy | z | y |
| 2 | Model | 4, 87 | 16.28 | <0.0001 | | | | |
| | Length | 1, 87 | 0.08 | 0.77 | | | | |
| | Method | 3, 87 | 20.77 | <0.0001 | z | y | zy | x |
| 3 | Model | 4, 87 | 11.63 | <0.0001 | | | | |
| | Length | 1, 87 | 2.05 | 0.16 | | | | |
| | Method | 3, 87 | 15.44 | <0.0001 | z | z | z | y |

are stocked. Hatchery-reared fish are usually considerably larger at age 1 or 2 than their naturally produced counterparts. For example, more than 80% of the stocked fingerlings in Missouri exceed 8 in at age 1 or 2 (Eder et al. 1997), whereas naturally produced fish average less than 6.7 in at age 2 in Missouri waters (Marzolf 1955; Graham and DeiSanti 1999). Hence, stocked and naturally produced fish could be distinguished by their length at age 1 or 2. For example, Siegwarth (1994) used back-calculated growth increments on pectoral spine sections to separate stocked from naturally produced channel catfish in the Buffalo River, Arkansas. Our findings suggest that some hatchery-reared fish could be misidentified as naturally produced fish using the traditional Dahl–Lee model for SP because this method severely underestimates length at age 1. However, the SPH model for SL may be useful in separating these groups of fish because it provides much more accurate length data at young ages.

In summary, we found no advantage in using otoliths over pectoral spines for back-calculation. Although otoliths may produce more accurate and precise age information than spines (Buckmeier et al. 2002), they do not appear to be as useful for back-calculation for channel catfish. Growth increments on pectoral spine sections were much easier to view and measure and provided the most accurate length and growth increment data. Using otoliths also requires

sacrificing the fish, whereas, removing pectoral spines has been shown to cause negligible mortality (Stevenson and Day 1987; Michaletz 2005; this study). We acknowledge that our findings were under rather ideal circumstances in that the actual age of the fish was known. Thus, all fish were accurately aged with both pectoral spines and otoliths. Errors in age estimation could have resulted in additional errors in estimating length and growth increments, and age estimation errors could be more prevalent when one is estimating the ages of older fish with spines rather than otoliths. Obviously, the ages of fish need to be accurately determined for back-calculation estimates to be valid. Perhaps otoliths could be collected from a subsample of the fish used for back-calculation to confirm the ages estimated by pectoral spines. Nevertheless, our findings indicate that using pectoral spines for back-calculation is more appropriate than using otoliths. We recommend that the SPH linear model for SL be used to estimate length-at-age data. Either this model or the previously used Dahl–Lee model for SP is appropriate for estimating the last growth increment and the initial length–last growth increment relationship and should provide reasonable estimates.

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