Transactions of the American Fisheries Society 138:361–372, 2009

DOI: 10.1577/T08-098.1

[Article]

Lake Sturgeon Age Validation using Bomb Radiocarbon and Known-Age Fish

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Abstract.—Pectoral fin spines have been the accepted structure for estimating the age of various sturgeon species for nearly 100 years, though other structures have also been used (otoliths, pectoral girdle, scutes, and caudal fulcra). Accuracy of age estimates using any of these structures has not been validated, so we report the first use of bomb radiocarbon (^{14}C) assays to assess the validity of ages estimated using growth increments on pectoral fin spine and otolith frontal cross sections from lake sturgeon *Acipenser fulvescens*; we also assessed age estimates from pectoral fin spines of known-age lake sturgeon. Growth increments on pectoral fin spine cross sections underestimated true age of fish older than 14 years and error increased with age, whereas otoliths accurately estimated true age up to at least 52 years. Increment formation on pectoral fin spine and otolith cross sections from juvenile lake sturgeon (ages 2–11) was similar, although pectoral spines were clearer and easier to interpret. A power function (true age = [estimated age]$^{1.054796}$, where estimated age was determined from pectoral spines; $r^2 = 0.98$) provides a means for correcting existing age estimates obtained from lake sturgeon pectoral fin spines.

Although critical to effective use of fish age data, validation of the accuracy of growth increments counted on a bony structure used to estimate age (e.g., scales, fin rays, or otoliths) has often been neglected by fisheries biologists (Beamish and McFarlane 1983; Campana 2001). For example, of 372 papers on fish age estimation that were published between 1983 and 2001, only 15% actually validated the age of their respective fish species (Campana 2001).

The best method for validating the accuracy of fish age estimates is to individually mark fish at a point in their life when their true age is known or can be reasonably approximated and to capture the fish later in life for age estimation (Campana 2001). Bomb radiocarbon (^{14}C) dating generally provides the best method for validating the age of long-lived fish. A sharp increase in atmospheric ^{14}C in the late 1950s from nuclear testing led to increased ^{14}C levels in organisms living at that time. Otolith cores of fish hatched before 1958 contain very low amounts of ^{14}C, whereas otolith cores from fish hatched between 1958 and 1968 contain increasingly elevated levels that can be used to validate methods of age estimation (Campana 2001).

Sturgeon comprise a group of large-sized, long-lived, and late-maturing anadromous and freshwater fishes that are now seriously threatened throughout their Holarctic range due to overharvest and spawning and nursery habitat loss and fragmentation caused by the building of dams and pollution (WSCS 2005). Of 26 recognized species of sturgeon and related paddle-

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Received June 3, 2008; accepted November 16, 2008
Published online March 16, 2009

fishes of the order Acipenseriformes, 24 are listed as threatened to critically endangered and several populations are listed as extinct (Birstein 1993; IUCN 2008). Accurate age data are critical for the development of population models that will contribute to effective long-term management of sturgeon stocks.

Various structures from sturgeon have been used to estimate age, including bones from the pectoral girdle, scutes, caudal fulcra, otoliths, and the leading spine of the pectoral fin (Kler 1916; D'Ancona 1923; Harkness 1923; Holzmayer 1924; Probatov 1929; Schneberger and Woodbury 1944; Cuerrier 1951); the first one to two rays of the pectoral fin of all acipenserids are sheathed in dermal bone and are considered to be fin spines (Findeis 1997). The first attempts to estimate age of sturgeon were with bones from the pectoral girdle (cleithrum and claviculum) but were relatively unsuccessful due to problems with bone resorption (Kler 1916). Kler (1916) concluded that cross sections of pectoral fin spines showed great potential for estimating age of four sturgeon species: Russian sturgeon *Acipenser gueldenstaedtii*, stellate sturgeon *Acipenser stellatus*, sterlet *Acipenser ruthenus*, and beluga *Huso huso*. However, Kler (1916) suggested that the age be verified using at least one additional bone. Pectoral fin spine sections of sterlet raised in captivity at seasonal temperatures for 1–10 years had the same number of growth increments on the sections as the number of years of growth (Holzmayer 1924). Harkness (1923) used whole sagittal otoliths to estimate the age of lake sturgeon *Acipenser fulvescens* from Lake Winnipeg, Manitoba, but did not validate the estimated ages. Growth increments on pectoral fin spine sections of European sea sturgeon *A. sturio* from the Guadalquivir River in Spain were distinct up to age 8 or 9 but became narrower and less distinct at older ages (Classen 1949). Average length at age from back-calculation of growth increments on fin spine sections corresponded well to measured lengths at estimated age (Cuerrier 1951), but this would be regarded today as age corroboration rather than age validation (Campana 2001).

Previous work attempting to validate ages estimated from the bony structures of various sturgeon species has shown a consistent pattern among species, where ages estimated from pectoral fin spines are accurate for younger fish but begin to lose their accuracy as the fish get older. For example, the number of pectoral fin spine growth increments outside the oxytetracycline (OTC) band equaled the number of years between OTC injection and recapture for 10 lake sturgeon (4–18 years old) from the Moose River in northern Ontario (Rossiter et al. 1995). Pectoral fin spine age estimates for older white sturgeon *Acipenser transmontanus* from the Columbia River, Washington, were unreliable (Rien and Beamesderfer 1994). Similarly, pectoral fin spine age estimates of older shovelnose sturgeon *Scaphirhynchus platorynchus* and pallid sturgeon *Scaphirhynchus albus* from the Missouri River system, Missouri and South Dakota, were also unreliable (Hurley et al. 2004; Whiteman et al. 2004).

Our primary objective was to determine whether age can be estimated accurately from lake sturgeon pectoral fin spines and otoliths. Here, we report the first application of ^{14}C as a dated marker for any sturgeon species. Our secondary objective was to compare growth increment formation on pectoral fin spines and otoliths of juvenile lake sturgeon younger than age 14.

Methods

Study area.—The Winnebago system is a large, shallow, eutrophic, riverine–lake system in east-central Wisconsin. Lake Winnebago and the three upriver lakes (Butte des Morts, Winneconne, and Poygan), collectively known as the Winnebago pool lakes, comprise 668 km^2 of surface water and are situated at the lower end of a 15,540-km^2 watershed through which flow the Wolf River and upper Fox River systems. The lower 200 km of the Wolf River (along with its major tributaries) and 60 km of the upper Fox River contain spawning and nursery grounds for the lake sturgeon population in the Winnebago system.

Known-age fish.—The term "known age" in this study applies to lake sturgeon that were tagged when their age was known or could be reasonably approximated from their size (Campana 2001). The term "true age" refers to the age determined from (1) the number of years for which recaptured, known-age fish were at large and (2) bomb ^{14}C analysis of otolith cores from individual fish. We examined the accuracy of pectoral fin spine age estimates of known-age fish and of fish whose true ages were estimated by bomb ^{14}C analysis of otolith cores. For adults, we also examined the accuracy of ages estimated from otolith cross sections by comparing these ages with those determined by the bomb ^{14}C assays. We compared increment formation and estimated age between pectoral fin spines and otoliths of lake sturgeon younger than age 14. All lake sturgeon were sampled during population and harvest assessments conducted on the Winnebago system.

Forty-six juvenile lake sturgeon (60–100 cm total length [TL]) were captured, measured to the nearest 1.3 cm, and marked with Monel tags attached to the base of their dorsal fins during bottom-trawl assessment surveys from 1976 to 1997 on Lake Winnebago. These fish were recaptured in winter spear harvest assessments from 1995 to 2004 (i.e., from 2 to 25 years after initial capture) and were sampled for age (pectoral fin

TABLE 1.—Estimated number of fish sampled (*N*) and mean, SD, range, and 95% confidence limits (CLs) of total length (TL) at ages 1–14 for juvenile lake sturgeon sampled in the Winnebago system, Wisconsin, during 1951–2007. Ages were estimated from pectoral fin spine sections.

					95% CL (cm)	
Age (years)	*N*	Mean TL (cm)	SD (cm)	Range (cm)	Lower	Upper
1	13	22.2	3.2	16.0–26.2	20.3	24.1
2	46	35.8	6.3	23.9–49.8	33.9	37.7
3	49	51.8	5.9	38.6–71.1	50.1	53.4
4	126	63.3	4.3	49.5–73.7	62.6	64.1
5	136	72.8	7.3	50.5–86.4	71.5	74.0
6	103	79.3	7.6	63.5–96.5	77.8	80.8
7	92	82.7	7.7	68.8–99.1	81.1	84.3
8	78	83.7	7.3	71.1–99.1	82.0	85.3
9	55	85.3	6.3	73.7–102.6	83.6	87.0
10	48	89.6	7.6	74.9–111.8	87.4	91.8
11	36	91.3	6.2	81.3–108.5	89.2	93.4
12	36	95.0	5.1	84.6–103.5	93.3	96.7
13	26	100.0	8.0	86.4–122.4	96.7	103.2
14	24	100.7	6.4	89.2–121.9	98.0	103.4

spine). These fish were not sampled for otoliths because only pectoral fin spines were collected at that time as part of the annual standardized harvest assessment. Two passive integrated transponder (PIT) tagged juvenile lake sturgeon stocked in 2001 and 2004 in the Winnebago system were recaptured in 2007 in trawls and were sampled for age (pectoral fin spines and otoliths).

Because ages estimated from pectoral fin spines have been validated for sterlet up to age 10 (Holzmayer 1924) and corroborated for lake sturgeon up to age 15 (Rossiter et al. 1995), we presumed that mean lengths at age from 868 lake sturgeon sampled in the Winnebago system during 1951–2007 (estimated age from pectoral fin spines $\leq$14 years; 16–122 cm TL) could be used to approximate age at initial tagging for the 46 recaptured juvenile fish. Fish that were 100 cm or less at initial capture were highly likely to be no older than 14 years; this allowed us to estimate their ages to within 1–4 years based upon empirical length-at-age data (Tables 1, 2; Figure 1). We calibrated age at capture and recapture to the nearest 0.01 year using year-specific hatching dates determined through spawning assessments on the Winnebago system (Folz and Meyers 1985; Bruch and Binkowski 2002). We estimated true age by adding the number of years at large (i.e., from tagging to recapture) to the estimated age at initial capture. We believed that an initial measurement error of 1–4 years was acceptable given the longevity of lake sturgeon and given that there was an average of more than 15 years between initial tagging and recapture of the 46 known-age wild fish. We recognized the limitations of using length to estimate age of fish, primarily due to the multiplicative error associated with length-at-age data. However, for lake sturgeon from the Winnebago system, we believe our estimated error was within a range that still allowed us to assign an estimate of age at initial capture to juvenile fish in our known-age sample.

We did not have sufficient length-at-age data from fish sampled during 1964–2007 to evaluate whether length at age for juveniles of ages 1–14 declined during 1951–2007. However, we were able to examine lengths at age (pectoral fin spine estimates) of 15-year-old fish sampled in the Winnebago lake sturgeon spear harvests during 1953–1959 and 1997–2006; these were periods with similar fisheries and harvest assessment methodology. We compared lengths of age-15 fish from these periods because fish younger than age 15 were not fully recruited to the fishery. Age 15 was 1 year older than the target range of juveniles from our original sample (ages 1–14) but should still be representative of overall growth of juveniles up to that age.

At recapture, all fish sampled during harvest seasons were measured to the nearest 1.3 cm TL, weighed to the nearest 0.23 kg, and sexed and staged for maturity according to criteria developed by Bruch et al. (2001). Pectoral fin spines to be used in age estimation were collected at the time of recapture. Known-age, PIT-tagged, stocked fish recaptured from Lake Winnebago with a bottom trawl during annual fish community assessments in August–October 2007 were sampled to determine TL to the nearest millimeter, weight to the nearest gram, sex, and age (pectoral fin spines and otoliths). After collection and initial cleaning, pectoral fin spines were dried in a cabinet dryer with air circulated at 20–25°C for 1 week. A 0.5-mm section was cut using an Isomet low-speed saw immediately distal to the basal propterygium and was examined by an experienced sturgeon age reader with reflected and

TABLE 2.—Original tagging date (1976–1997); sex; total length (TL) and assigned age (years) at tagging; recapture date (1995–2004); TL at recapture; number of years at large; true age at recapture; and recapture age estimated from pectoral fin spines of juvenile lake sturgeon sampled in the Winnebago system, Wisconsin. Assigned ages are based on the within-year birth date determined from spawning survey data.

Original tagging date	Sex	TL (cm) at tagging	Assigned age at tagging	Recapture date (when aged)	TL (cm) at recapture	Years at large	True age at recapture	Pectoral spine age at recapture
18 Apr 1976	♀	94.0	11.95	10 Feb 2001	165.1	24.82	36.77	32.77
8 May 1978	♀	99.1	13.01	17 Feb 1995	162.6	16.78	29.79	26.79
16 May 1978	♂	96.5	12.03	9 Feb 2002	143.5	23.74	35.77	25.77
10 Jul 1978	♀	68.6	4.18	18 Feb 1995	124.5	16.61	20.79	18.79
12 Jul 1978	♀	83.8	8.19	13 Feb 1997	141.0	18.59	26.78	22.78
12 Jul 1978	♂	88.9	10.19	11 Feb 1996	125.7	17.58	27.77	18.77
12 Jul 1978	♀	91.4	11.19	26 Feb 1995	152.4	16.63	27.82	25.82
31 Aug 1978	♀	91.4	11.32	12 Feb 1995	152.4	16.45	27.78	23.78
19 Oct 1978	♂	69.9	4.46	16 Feb 1995	129.5	16.33	20.79	19.79
25 Sep 1979	♀	92.7	12.39	12 Feb 2000	154.9	20.38	32.78	29.77
27 Sep 1979	♂	99.1	13.40	10 Feb 2001	156.2	21.37	34.77	27.77
10 Oct 1979	♂	100.3	14.43	15 Feb 1996	134.6	16.35	30.78	21.78
11 Oct 1979	♂	100.3	14.44	10 Feb 2001	146.1	21.34	35.77	26.77
11 Sep 1980	♀	95.3	12.35	15 Feb 2004	135.9	23.43	35.78	26.78
18 Sep 1980	♂	81.3	6.37	12 Feb 2000	132.1	19.40	25.77	22.77
8 Oct 1980	♀	96.5	12.43	14 Feb 2004	133.4	23.35	35.78	22.78
10 Oct 1980	♀	97.8	13.43	15 Feb 2004	154.9	23.35	36.78	34.78
28 Oct 1980	♀	91.4	11.48	14 Feb 2004	144.8	23.30	34.778	26.78
4 Nov 1980	♂	96.5	12.50	13 Feb 1999	111.8	18.28	30.776	25.78
5 Nov 1980	♀	88.9	10.50	17 Feb 1998	149.9	17.28	27.788	22.79
28 Sep 1981	♂	99.1	13.40	12 Feb 2000	124.5	18.37	31.773	25.77
29 Sep 1981	♀	90.2	11.40	14 Feb 1998	127.0	16.38	27.780	21.78
12 Oct 1981	♂	83.8	8.44	14 Feb 2004	120.7	22.34	30.779	19.78
12 Oct 1981	♂	90.2	11.44	12 Feb 2000	102.9	18.34	29.773	12.77
12 Oct 1981	♂	90.2	11.44	12 Feb 2000	96.5	18.34	29.773	13.77
13 Oct 1981	♂	95.3	12.44	14 Feb 2004	146.1	22.34	34.779	26.78
16 Oct 1981	♀	91.4	11.45	15 Feb 1998	115.6	16.33	27.783	19.78
21 Oct 1981	♂	86.4	8.46	15 Feb 2004	118.1	22.32	30.782	18.78
21 Oct 1981	♀	91.4	11.46	18 Feb 1995	132.1	13.33	24.791	20.79
18 Oct 1982	♂	76.2	5.45	15 Feb 2004	123.2	21.33	26.782	23.78
7 Oct 1983	♀	95.3	12.43	15 Feb 1998	129.5	14.36	26.784	20.78
26 Sep 1984	♂	99.1	13.39	11 Feb 1995	121.9	10.38	23.771	16.77
14 Sep 1987	♂	80.0	6.36	13 Feb 2000	96.5	12.42	18.778	13.78
14 Sep 1987	♀	99.1	13.36	15 Feb 2004	133.4	16.42	29.783	26.78
2 Aug 1994	♂	84.6	8.24	12 Feb 2000	95.3	5.53	13.774	12.77
3 Aug 1994	♂	94.5	12.25	14 Feb 2004	129.5	9.53	21.780	20.78
3 Aug 1994	♂	99.6	13.25	13 Feb 1999	121.9	4.53	17.778	20.78
4 Aug 1994	♀	91.9	11.25	13 Feb 2003	114.3	8.53	19.778	20.78
9 Aug 1994	♂	79.2	6.26	10 Feb 2002	101.6	7.51	13.770	12.77
10 Aug 1994	♂	97.8	13.27	12 Feb 2000	109.2	5.51	18.774	13.77
11 Aug 1994	♂	94.0	12.27	12 Feb 2000	104.1	5.51	17.774	12.77
23 Aug 1994	♂	88.9	10.30	10 Feb 2001	124.5	6.47	16.771	16.77
23 Aug 1994	♂	91.4	11.30	10 Feb 2001	114.3	6.47	17.771	17.77
11 Aug 1997	♀	90.2	11.27	13 Feb 2000	91.4	2.51	13.776	14.78
11 Aug 1997	♂	92.7	12.27	15 Feb 2004	120.7	6.51	18.782	20.78
13 Aug 1997	♀	100.3	14.27	12 Feb 2000	110.5	2.50	16.773	18.77

transmitted light under a binocular scope at 7–25× magnification to estimate the number of growth increments present.

Otoliths were extracted from the auditory capsules in the neurocranium, dried, and embedded in a slow-drying hard epoxy (Araldite epoxy GY502 and hardener HY956 in a 5:1 weight ratio). A 0.5-mm frontal section was cut from the core (Figure 2) using two blades separated by spacers on an Isomet low-speed, diamond-bladed saw. Sections were lightly polished to improve their visibility under magnification. While under a binocular microscope at 16–40× magnification using reflected light, growth increments were digitally photographed at a resolution of 2,048 × 2,048 pixels and then were digitally enhanced using Adobe Photoshop CS2. Age was interpreted from the digital images; each pair of adjacent opaque and translucent bands was called an annulus (the opaque bands appeared white under reflected light). Two experienced readers independently estimated age from pectoral fin spines and otoliths of each fish.

Bomb radiocarbon.—Sagittal otolith pairs and pectoral fin spines were collected from 22 of the largest lake sturgeon registered during the 2006 and

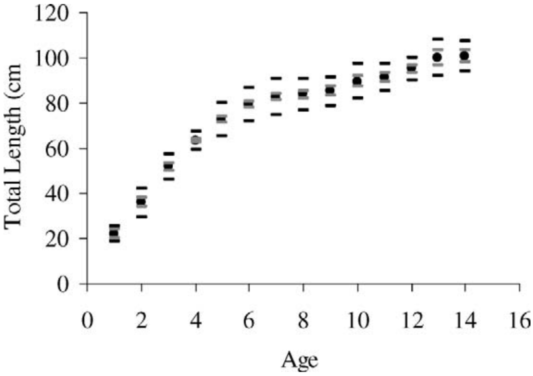

FIGURE 1.—Estimated total length at age 1–14 for juvenile lake sturgeon in the Winnebago system, Wisconsin, 1951–2007 (gray bars represent 95% confidence intervals; black bars represent ±SD).

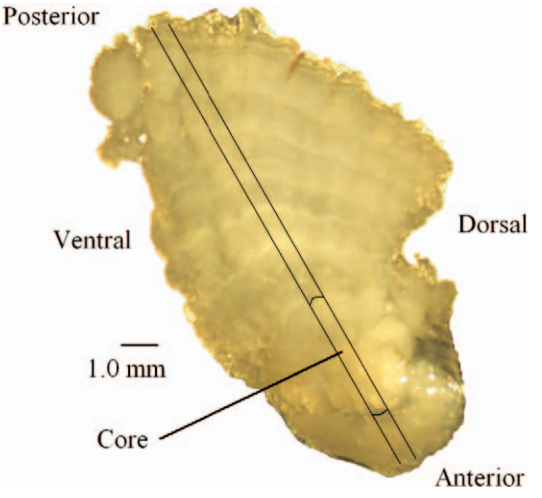

FIGURE 2.—Lake sturgeon sagittal otolith, showing orientation, location of frontal section removed for age estimation, and core removed for bomb radiocarbon (^{14}C) assay.

2007 winter spear harvest seasons on Lake Winnebago. All fish were measured to the nearest 1.3 cm TL, weighed to the nearest 0.23 kg, and sexed and staged for maturity. Ages estimated from pectoral fin spines indicated that the birth year of each sampled fish was probably before 1970. Five of these lake sturgeon otolith pairs were too porous or crystalline to assay or age, but 17 bomb ^{14}C assays were successfully completed, of which three were too poor to estimate age accurately from increment counts.

Otolith cores representing what was assumed to be the first 1–6 years of life were isolated from the central section of each otolith pair as a solid piece with a Merchantek computer-controlled micromilling machine using a 300-μm-diameter steel drill bit. In some lake sturgeon, additional core material from the same otolith was isolated from the two adjacent sections but was restricted to the innermost increments around the core to allow for offset of these lateral sections from the primordium. This procedure of obtaining material from both otoliths of the pair and occasionally from multiple sections per otolith was necessary to obtain at least 3 mg of core sample material for assay from each lake sturgeon. The date of sample formation was calculated as the year of fish collection minus the age span of the fish as determined from the edge of the otolith to the midpoint of the range of growth increments present in the extracted core. Growth increments appeared to be regularly spaced in the first 6 years of life, thereby indicating that the midpoint of the core increments was a suitable choice for the mass-weighted midpoint of otolith core deposition. After sonification in purified water (Super Q system, Millipore) and drying, the sample was weighed to the nearest 0.1 mg in preparation for ^{14}C assay by means of accelerator mass spectrometry (AMS). The AMS assays also provided δ^{13}C (‰) values to correct for isotopic fractionation effects and provide information on the source of the carbon. Radiocarbon values were subsequently reported as Δ^{14}C, which is the per-mille (‰) deviation in ^{14}C of the sample from the ^{14}C concentration of 19th-century wood, corrected for sample decay occurring before 1950 (methods of Stuiver and Polach 1977). The mean standard deviation (SD) of the individual ^{14}C assays was about 5‰.

The year of formation of the sturgeon otolith core can be estimated by comparing its ^{14}C content with that of a reference ^{14}C chronology based on known-age material. The marine Δ^{14}C reference chronologies used in many other otolith studies are not appropriate for use in a freshwater fish species (Kalish 1993); therefore, the lake sturgeon ^{14}C assays were compared with two independent reference chronologies based on otolith cores from freshwater fish: (1) Arctic char *Salvelinus alpinus* and lake trout *Salvelinus namaycush* from the Arctic (Campana et al. 2008) and (2) freshwater drum *Aplodinotus grunniens* from Lake Winnebago (Davis-Foust et al. 2009, this issue). Although the freshwater drum chronology was not a chronology based on known-age material, freshwater drum otoliths are well known for their clear and easily interpreted growth pattern, which suggests that the date of formation of their cores can be accurately determined (Pereira et al. 1995).

The feature of a bomb ^{14}C chronology that best serves as a stable dated reference mark is the year of initial increase above prebomb levels in response to the period of atmospheric testing of nuclear weapons. Comparison of this year of initial increase in the reference chronology with that of the species being tested (in this case, lake sturgeon) provides the best measure of age estimation accuracy, because consistent over- or underestimation of age will shift the calculated year of initial increase in the test chronology to earlier or more recent years. Several possible methods can be used to calculate and compare the timing of increase between reference and test chronologies, including a promising analytical approach by Hamel et al. (2008). A quantitative but simpler approach is to define the year of initial increase that is consistent with atmospheric sources, whereby a Δ^{14}C value that is 10% above the prebomb background is used to identify the year of initial appearance of bomb Δ^{14}C (Y_T; Campana et al. 2008). The calculation was based on the difference in Δ^{14}C values between peak and prebomb values. Specifically, the value corresponding to the 10% threshold contribution of Δ^{14}C (C_T) was estimated by subtracting 90% of the range in Δ^{14}C between its lowest value (C_L) and peak (C_P) value from the C_P as follows:

$$C_T = C_P - 0.9(C_P - C_L),$$

where C_L is on or after 1952, the year of initial appearance of bomb ^{14}C in the atmosphere. The Y_T is then defined as the year in which the loess-fitted Δ^{14}C chronology first exceeds C_T.

We estimated a ^{14}C-based fish age—independent of any counts of growth increments—for otolith cores with Δ^{14}C values above the prebomb level as the fish age that was required to move the Δ^{14}C assay value laterally onto the loess fit of the freshwater drum reference chronology. We considered ^{14}C-based fish age as true age, although it includes analytical error around the ^{14}C assay value (error of about 5‰, corresponding to ~0.5 year) and assumes a linear increase in ^{14}C through the period of otolith core formation (which would introduce an error of up to 1 year if the increase was exponential). Several otoliths for which the section image was classified as poor (independent of the ^{14}C assay results) were not included in this calculation.

Early increment formation and corroboration of age estimates.—Twelve wild and two stocked juvenile lake sturgeon less than 90 cm TL were captured from Lake Winnebago with a bottom trawl during standardized annual fish community assessments in August–October 2007. Fish were measured to the nearest millimeter and weighed to the nearest gram, and pectoral fin spines and otoliths were collected for age estimation. Pectoral fin spines and otoliths were prepared and age was estimated using the methods described above. Four experienced readers examined growth increment formation on pectoral fin spine and otolith sections of the juvenile lake sturgeon and independently estimated increment location and age. All examinations and age estimates were made by individuals without prior knowledge of fish size or origin.

Data analysis.—We used known ages and ^{14}C-based ages as true ages in an age bias plot, which is the method that is most sensitive to linear and nonlinear differences (Campana et al. 1995), to compare mean ages estimated from pectoral fin spines with true ages of individual known-age and ^{14}C-assayed lake sturgeon. We plotted individual otolith ages against true ages to examine the accuracy of ages estimated from otolith cross sections. We used coefficient of variation (CV = 100 × SD/mean) to measure precision of age estimates based on otoliths and pectoral fin spines from juvenile lake sturgeon less than 90 cm, and we plotted individual otolith age estimates against pectoral fin spine age estimates to compare juvenile ages estimated from the two structures. To examine the potential for correcting historic age estimates from pectoral fin spines, we fitted linear (intercept = 0), exponential, and power function models of true age against estimated age (pooled known-age and ^{14}C samples). We examined residuals and r^2 values to select the model with the best fit. We used a likelihood ratio test to determine whether true age–estimated age models differed significantly between male and female lake sturgeon.

Results

We found no significant difference between mean (±SD) TL at age 15 during 1953–1959 (114.3 ± 8.7 cm) and 1997–2006 (114.3 ± 8.6 cm; $t = 0.049$, df = 533). We concluded that growth rates of juveniles were similar, thereby allowing us to pool the 1951–2007 length-at-age data from juveniles of ages 1–14 for use in estimating length-based age of the 46 known-age juveniles.

Estimated age (mean ± SD) at initial capture of known-age fish ranged from 4 ± 1 to 14 ± 4 years. Years at large between marking and recapture averaged (±SD) 15.4 ± 6.6 years and ranged from 2.5 to 24.8 years (Table 2). Ages estimated from pectoral fin spines were generally less than true ages; the average difference was −4.96 ± 4.57 years, and differences ranged from +2 to −17 years (Table 2). Ages estimated from pectoral spines of two PIT-tagged, stocked fish (6 and 3 years) were the same as the true ages of the fish, whereas ages estimated from otoliths were 6 and 3 or 4 years, respectively (different estimates from the two readers).

The ^{14}C chronology derived from lake sturgeon

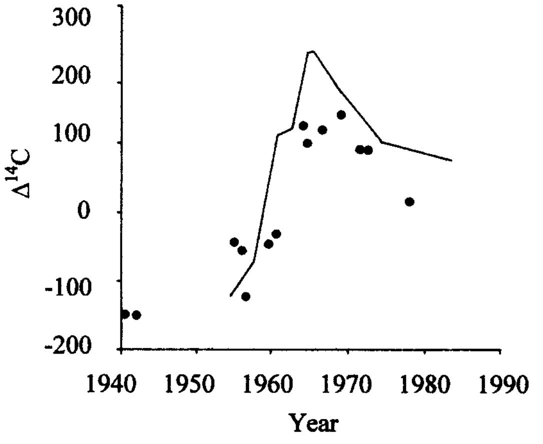

FIGURE 3.—Values of $\Delta^{14}C$ (per-mille [‰] deviation in radiocarbon [^{14}C] of the sample from the ^{14}C concentration of 19th-century wood, corrected for pre-1950 decay) for otolith cores of lake sturgeon sampled from Lake Winnebago, Wisconsin (2006–2007), and year of core formation based on otolith age estimates (black circles); also included is a $\Delta^{14}C$ reference chronology (solid line fit through loess procedure) for freshwater drum from Lake Winnebago (Davis-Foust et al., this issue).

otoliths closely resembled the Lake Winnebago $\Delta^{14}C$ reference chronology developed from freshwater drum otolith cores (Davis-Foust et al., this issue; Figure 3). Because the lake sturgeon chronology would have been phase shifted (to the right or left) if growth increment counts had under- or overestimated age, these results confirmed that on average, otolith increment counts provided an accurate age estimate. However, the feature of a bomb ^{14}C chronology that best serves as a dated reference mark is the year of initial increase above prebomb levels in response to the period of atmospheric testing of nuclear weapons. For the two available freshwater reference chronologies, the Y_T was calculated as being 1957 or close to 1957. Calculation of the lake sturgeon Y_T indicated that ^{14}C first increased 1 year earlier (i.e., in or around 1956). This 1-year offset is within the 1–3-year range of uncertainty associated with bomb chronologies, thereby supporting the conclusion that lake sturgeon growth increments were interpreted accurately on average.

Bomb ^{14}C-derived ages of assayed lake sturgeon ranged from 27 to 52 years (±1–3 years; Table 3). The key samples for comparison were cores formed before 1966, during a period when environmental $\Delta^{14}C$ levels changed most rapidly. Cores that formed during the 1940s and were 67–68 years old based on increment counts were clearly from the prebomb period based on $\Delta^{14}C$; therefore, these fish must have been at least 52 years old. Matching pectoral fin spine cross sections had 47 and 48 annuli, respectively. Four other core samples that were dated between 1958 and 1961 based on increment counts of 39–47 years were also dated by $\Delta^{14}C$ as having formed between 1960 and 1961; 2–4-year deviations from the fitted line occurred in both directions. Cores formed after about 1964 were characterized by $\Delta^{14}C$ values that were clearly from the postbomb period but were somewhat lower and parallel to the corresponding freshwater drum reference chronology. Postbomb $\Delta^{14}C$ magnitudes often differ between water masses due to differences in carbon turnover and water mixing rates, and so they are difficult to use as indicators of the individual year of formation. However, the timing of increase or decrease should still parallel that of the reference chronology, which is the case here. Therefore, our results validate the interpretation of lake sturgeon otolith increments as accurate age indicators to an age of at least 52 years but with individual age estimation error of up to 4 years.

Ages estimated from pectoral fin spines were generally less than true ages after about age 14, and the deviation increased as fish grew older (Figure 4). Ages estimated from otoliths were strongly correlated to true ages of known-age and ^{14}C-assayed fish ($r^2 = 0.98$; Figure 5). Ages estimated from pectoral spines diverged from ages estimated from otoliths of older fish (age bias plot is not shown but was nearly identical to Figure 4). Examples of otolith cross sections showing annual growth increments from a known-age, 6-year-old, stocked fish; a 9-year-old wild juvenile; and a 34-year-old, bomb ^{14}C-aged fish are illustrated in Figure 6.

Early Increment Formation and Corroboration of Age Estimates

Growth increments were relatively apparent on pectoral fin spine and frontal otolith sections from the 12 wild and 2 stocked juvenile lake sturgeon sampled for age (Table 4; Figure 6). Age estimation precision was higher for pectoral fin spines (CV = 0%) than for otoliths (CV = 14.0%). Identifying the first increment was more difficult in otolith sections. Estimated ages from pectoral fin spines were strongly correlated to ages from otoliths for the 14 juvenile lake sturgeon (Figure 7).

Model of True Age versus Estimated Age

A power function (true age = [estimated age]$^{1.054796}$) provided the best fit between estimated pectoral fin spine age and true age ($r^2 = 0.98$; $F = 18{,}826.7$; df = 1, 62; $P < 0.001$), and model residuals were randomly distributed around zero (Figure 8). Linear and exponential models also described a high fraction of error in estimated age ($r^2 = 0.96$ and 0.93, respective-

TABLE 3.—Sample date, sex, total length (TL), age (years) estimated from pectoral fin spines or otoliths, true age determined from bomb radiocarbon (^{14}C) assay of otolith cores, $\Delta^{14}C$ value (per-mille [‰] deviation in ^{14}C of the sample from the ^{14}C concentration of 19th-century wood, corrected for pre-1950 decay), and year of otolith formation based on either increment counts or $\Delta^{14}C$ values for adult lake sturgeon sampled in the Winnebago system, Wisconsin, 2006–2007. Asterisks indicate fish that could not be assigned a year of otolith formation based on $\Delta^{14}C$ because values pre-dated 1958 levels.

Sample date	Sex	TL (cm)	Pectoral spine age (years)	Otolith age (years)	^{14}C (true) age (years)	$\Delta^{14}C$ value	Year of formation (based on increment counts)	Year of formation (based on $\Delta^{14}C$ value)
Feb 2006	♂	137.2	32	27	27.0	16.6	1978	1978
Feb 2006	♀	162.6	40	38	37.0	126.4	1964	1965
Feb 2006	♂	162.6	32	34	38.5	91.4	1972	1968
Feb 2006	♀	161.3	37	39	39.0	84.3	1968	1968
Feb 2006	♀	166.4	35	36	39.5	91.3	1971	1968
Feb 2006	♂	153.7	38	42	42.0	101.6	1964	1964
Feb 2006	♀	167.6	39	42	42.5	120.6	1966	1966
Feb 2006	♀	161.3	35	40	43.0	141.4	1969	1966
Feb 2006	♂	146.1	39	48	44.5	−42.7	1955	1958
Feb 2006	♀	176.5	39	39	46.0	−44.2	1967	1960
Feb 2006	♀	162.6	34	47	47.0	−45.9	1959	1959
Feb 2006	♀	165.1	40	48	48.0	−30.5	1960	1960
Feb 2006	♀	160.0	35	49	49.0	−122.1	1956	1956
Feb 2006	♀	165.1	35	48	50.0	−117.5	1959	1957
Feb 2007	♀	188.0	52	54	52.0	−54.0	1956	1958
Feb 2006	♀	179.1	47	67	>52	−149.9	1940	*
Feb 2006	♀	170.2	48	68	>52	−149.8	1942	*

ly), but residuals were not linearly distributed. The power function model predicted that lake sturgeon with estimated ages of 20, 40, and 60 years had actual ages of 24, 50, and 75 years, respectively. Relationships between true age and estimated age did not differ significantly between male and female lake sturgeon ($F = 1.20$; df = 1, 62; $P = 0.28$).

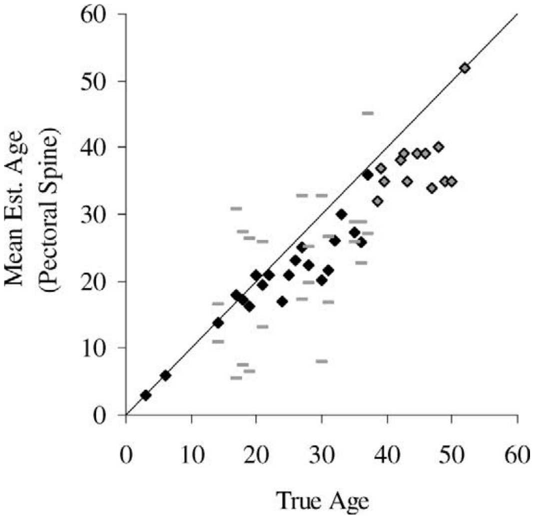

FIGURE 4.—Age bias plot comparing mean estimated age (years) from pectoral fin spines with the true age of known-age lake sturgeon (1995–2004; black diamonds) or with the true age determined through bomb radiocarbon assays of otolith cores (2006–2007; gray diamonds) from lake sturgeon sampled in the Winnebago system, Wisconsin. Gray bars delineate 95% confidence intervals around mean estimated ages for true ages sampled more than once. The 1:1 line is also illustrated.

Discussion

We found that lake sturgeon ages estimated from pectoral fin spines were accurate up to age 14 but underestimated true age beyond age 14. The belief over the last 100 years that annual growth increments are

FIGURE 5.—Age (years) estimated from frontal otolith cross sections compared with true age derived from known-age fish (1995–2004) or from bomb radiocarbon assays of otolith cores (2006–2007) from lake sturgeon sampled in the Winnebago system, Wisconsin. The 1:1 line is also illustrated.

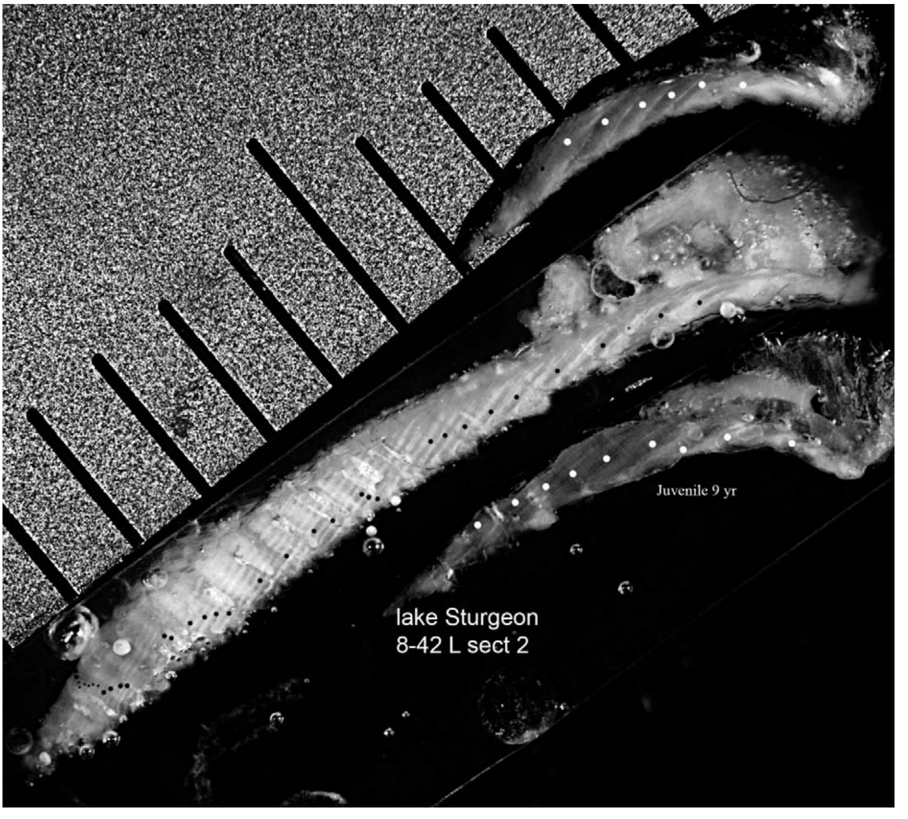

FIGURE 6.—Otolith cross sections (with growth increments) from adult and juvenile lake sturgeon collected in the Winnebago system, Wisconsin. Age estimates are 34 (large section in middle: bomb radiocarbon-aged fish sampled in February 2006), 9+ (bottom section: wild juvenile sampled in August 2007), and 6+ (top section: known-age, stocked fish sampled in August 2007) years. Rule is in millimeters.

TABLE 4.—Collection date, total length (TL), and age (years) estimated from pectoral fin spines (PFS) and otoliths (two readers per structure) of juvenile lake sturgeon sampled from Lake Winnebago, Wisconsin (August–October 2007), for growth increment formation and corroboration. Values in bold describe known-age fish. Asterisks denote fish whose otoliths were too porous to use in age estimation. All ages were estimated by counting to the last visible annuli (i.e., growth to the edge is not included).

		PFS		Otolith	
Date collected	TL (cm)	Reader 1	Reader 2	Reader 1	Reader 2
1 Aug	86.0	9	9	9	9
8 Aug	**74.9**	**6**	**6**	**6**	**6**
8 Aug	59.9	3	3	3	3
29 Aug	63.8	4	4	4	4
29 Aug	76.2	7	7	8	7
31 Aug	76.5	6	6	7	6
4 Sep	88.9	9	9	*	*
4 Sep	79.5	11	11	9	9
4 Sep	**64.0**	**3**	**3**	**4**	**3**
5 Sep	51.6	2	2	5	2
4 Sep	72.6	6	6	5	5
5 Sep	52.8	2	2	1	2
5 Sep	65.5	6	6	6	5
1 Oct	80.3	8	8	10	9

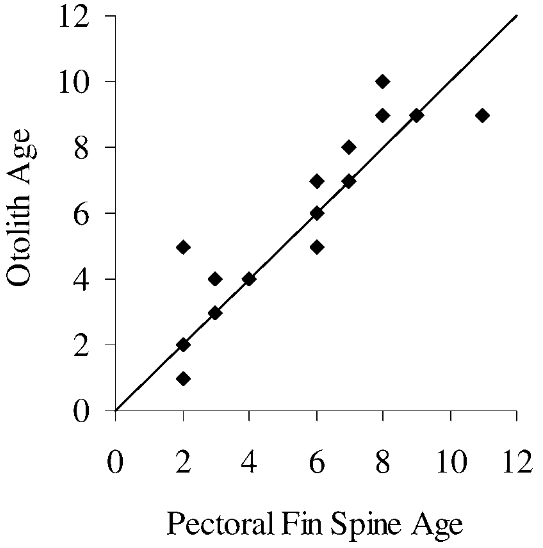

FIGURE 7.—Age estimates (years) based on otolith cross sections compared with age estimates based on pectoral fin spine sections from juvenile lake sturgeon sampled in the Winnebago system, Wisconsin, during August–October 2007. The 1:1 line is also illustrated.

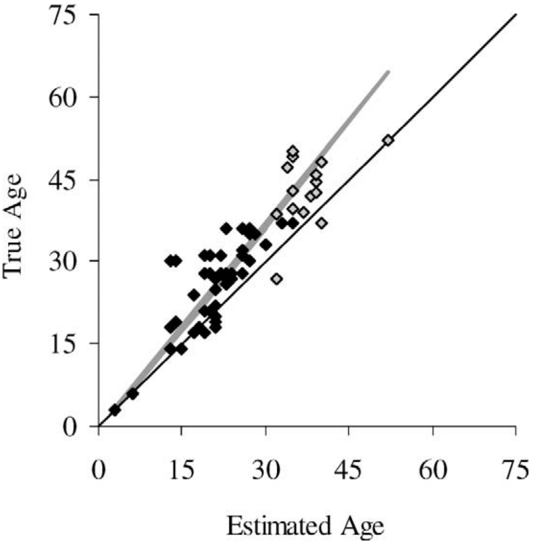

FIGURE 8.—Regression of true age versus estimated age based on examination of pectoral fin spines from lake sturgeon sampled in the Winnebago system, Wisconsin. True age is based on known-age fish (black diamonds) or bomb radiocarbon-assayed fish (gray diamonds). Gray line represents the power function model: true age = (estimated age)$^{1.054796}$. The 1:1 line (black line) is also illustrated.

deposited on pectoral fin spines of sturgeon has been based upon actual age validation of some younger ages (Holzmayer 1924), other studies that examined primarily young fish (where spines are more likely to be accurate), or studies that reported age corroboration instead of age validation (Cuerrier 1951; Probst and Cooper 1954; Brennan and Cailliet 1989; Rossiter et al. 1995; Stevenson and Secor 1999). Using underestimates of true age, especially with long-lived species like lake sturgeon, will result in overestimating total annual mortality rates. If natural mortality is equated to fishing mortality, allowable harvest rates will be set too high, thereby increasing the risk of overharvest. Given the serious consequences of using underestimates of age in population modeling, we advise caution in the use and application of sturgeon age estimates derived from pectoral fin spines. Our true age–estimated age correction model could be applied to pectoral fin spine age estimates from other sturgeon populations or species; however, the model's interpopulation and interspecific relevance will be unknown until other validation studies are completed.

The age at which inaccuracies become problematic may vary among sturgeon species and among populations within species. Our results suggest that inaccuracies for lake sturgeon from the Winnebago system begin at the onset of their protracted period of gonadal development (Bruch 1999; Bruch et al. 2001).

Pectoral fin spines may develop a new growth increment every year, but our ability to discern and interpret these increments may be hampered by one or more factors, including slow growth, individual variation, health of an individual or a population, sex, stage of sexual maturity, and short- or long-term environmental conditions. These factors could vary in their individual or combined effects (for populations or individuals within a population) on growth increment development or our ability to discern increments. Spine collection and processing techniques and the quality of equipment could also affect readability of cross sections from pectoral fin spines. Also, sturgeon pectoral fin spines actively resorb materials that have been laid down in previous increments and therefore may be not be suitable for biochronology (Veinott and Evans 1999). Resorption may be more of a problem as an individual fish grows into maturity and through adulthood; this is an important consideration when using these structures for estimating ages of fish belonging to long-lived species.

Since Schneberger and Woodbury's (1944) efforts, very little work using otoliths to estimate sturgeon age has been reported. Stevenson and Secor (1999) attempted to estimate age of Atlantic sturgeon *Acipenser oxyrinchus* by using sagittal sections of otoliths (similar to Schneberger and Woodbury 1944), but they felt that the optical contrast between opaque and translucent zones in the section was not sufficient to permit confident assignment of annual growth increments, especially in sections with more than 20 increments. Wide use of sturgeon otoliths may be limited because the fish must be killed to enable collection, the otoliths are very fragile, and 10–20% of otoliths may be too porous to section and read. Despite these difficulties, we encourage researchers to use otoliths (frontal section) for sturgeon age estimation when possible because these are probably the only structures that can provide an accurate age estimate throughout the lifetime of an individual sturgeon.

Acknowledgments

We thank the fisheries staff of the Upper Fox-Wolf Work Unit, Wisconsin Department of Natural Resources, for collecting the lake sturgeon heads; Cory Wienandt for assisting with sturgeon head processing and otolith extraction; Jack O'Brien for 35 years of sturgeon pectoral spine aging; Jamie Joudrey for embedding and sectioning otoliths; Sturgeon for Tomorrow for supporting travel for R.M.B. and S.L.D.F. to work with S.E.C. for 3 d on the project at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia; and all the Winnebago sturgeon spearers that donated their lake sturgeon heads for the study. This project was funded by the Wisconsin Department of Natural Resources Sturgeon Spearing License Fund.

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