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[Article]

Age Validation of Freshwater Drum using Bomb Radiocarbon

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Abstract.—The ages of freshwater drum *Aplodinotus grunniens* have typically been estimated by counting the growth increments on their scales or otoliths, but the accuracy of these estimates has not been validated. We used accelerator mass spectrometry (AMS) bomb radiocarbon dating to validate age estimates from sagittal otoliths of freshwater drum from the Lake Winnebago system, Wisconsin. The freshwater drum $\Delta^{14}C$ chronology from the AMS assay closely reflects the timing and shape of other bomb radiocarbon chronologies, thus validating the accuracy of otolith growth increments to at least age 52 ± 2 years. The progression of a strong 1983 year-class, which was detected every year sampled over the course of the study (1986, 2003–2007), and indices of year-class abundance calculated from trawling assessments on Lake Winnebago (1986–2007) corroborated otolith ages. Age estimate comparisons between scales, anal spines, dorsal spines, and otoliths showed scales and spines to be completely unreliable as aging structures after age 2. Freshwater drum live to very old ages relative to most other Great Lakes fishes; our oldest specimen based on an otolith age estimate was 58 years old.

Estimates of fish age are the foundation for understanding and forecasting fisheries population dynamics. Accurate age estimation is critical for correctly calculating age structure, growth rates, survival, mortality rates, and age at maturity (Ricker 1975; Campana 2001; Hoxmeier et al. 2001). The use of aging structures needs to be validated for all ages of a species since the frequency of increment formation may change during a fish's life history (Beamish and McFarlane 1983; Campana 2001).

Freshwater drum *Aplodinotus grunniens*, the only freshwater member of the family Sciaenidae, has the broadest latitudinal distribution of any freshwater fish species in North America (Stewart and Watkinson 2004; Rypel et al. 2006). Although not considered a sport fish, its common abundance makes it a significant member of many fish communities as a forage fish and multilevel predator. Stomach content analysis has revealed that small freshwater drum are eaten by walleye *Sander vitreus*, burbot *Lota lota*, sauger *S. canadensis* and white bass *Morone chrysops* in the Mississippi River and Lake Winnebago, Wisconsin (Priegel 1963, 1967; Butler 1965). Walleye and sauger, two of the most abundant piscivorous fishes in Lake Winnebago, had greater growth rates during years of high age-0 freshwater drum abundance, strongly suggesting that drum are an important prey item (Staggs and Otis 1996). Freshwater drum are benthic generalist feeders, and larger individuals will consume small fish (Daiber 1952; Becker 1983). In Lake Winnebago, midge larvae (Chironomidae) have historically been a primary component of freshwater drum diets (Priegel 1967), making this species a potential competitor with lake sturgeon *Acipenser fulvescens*, which are known to also depend heavily on chironomids (Choudhury et al. 1996; Stelzer et al. 2008).

Before 1994, most of the published demographic parameters for freshwater drum, such as growth rates, mortality rates, and age at maturity, were based on age estimates from scales (e.g., van Oosten 1938; Schoffman 1940; Daiber 1953; Houser 1960; Edsall 1967;

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Priegel 1969; Wrenn and Shoals 1969; Klaassen and Cook 1974; Becker 1983; Bur 1984). After 1994, sagittal otoliths became the most frequently used structure (e.g., Pereira et al. 1994, 1995; Palmer et al. 1995; Rypel et al. 2006; Rypel 2007), although some studies continued to use scales (e.g., Phelps et al. 2000; Braaten and Guy 2004). Ages estimated from otoliths have been used to determine maturation rates (Palmer et al. 1995), compare growth rates of freshwater drum from different habitats (Rypel et al. 2006), and detect sexual dimorphism (Rypel 2007). In addition, widths of otolith growth increments have been used in biochronological studies to investigate the influence of environmental conditions (Pereira et al. 1994, 1995) and community interactions (Ostazeski and Spangler 2001) on growth.

Despite their widespread use in estimating age, scales and otoliths of freshwater drum have not been validated as aging structures, thus weakening the credibility of studies that have used age estimates from these structures. Timing of annulus formation on freshwater drum scales has been evaluated, but without validation of age estimates (e.g., Swedberg 1965; Edsall 1967; Wrenn 1969). Goeman et al. (1984) reported age validation of freshwater drum using sagittal otolith age estimates to follow the progression of individuals in a strong year-class for three consecutive years, but this methodology is considered age corroboration, which can support but not replace age validation (Campana 2001). Also, anal and dorsal spines of freshwater drum have not been evaluated as valid aging structures.

The most unambiguous method for validating the periodicity of growth increments is using fish of known age (Beamish and McFarlane 1983; Casselman 1987; Campana 2001). This method is more difficult, though, for large populations of fish, fish located in larger water bodies, and long-lived fishes. Further, rough fish species like freshwater drum are generally considered undesirable and typically do not receive the attention nor the funding needed for intensive studies.

For long-lived fishes, the best alternative method for validating age estimates is assaying the cores of their otoliths for atomic bomb radiocarbon (Campana 2001). The thermonuclear bomb testing era in the 1950s and 1960s resulted in a spike in the quantity of radiocarbon (^{14}C) in the earth's hydrosphere, leaving a detectible temporal signature in otoliths and other calcified structures of organisms living in that era. Bomb radiocarbon dating does not use radioactive decay, as does the traditional method of radiocarbon dating; rather, it is a measure of the change in atmospheric radiocarbon that was released from atmospheric bomb testing and incorporated into carbon-based structures of growing organisms. Subsequently, bomb radiocarbon dating is best used on structures that (1) were growing during the bomb-testing era, (2) have visible growth increments from which to estimate age, (3) are metabolically inert after carbon deposition, and (4) provide enough material for ^{14}C assay (minimum of 3 mg). When large enough, the cores of fish otoliths that formed during the bomb-testing period meet these criteria.

Bomb radiocarbon dating has been completed on the otoliths of numerous marine and semimarine species but relatively few freshwater species. Marine species include haddock *Melanogrammus aeglefinus* (Campana 1997), red snapper *Lutjanus campechanus* (Baker and Wilson 2001), gray snapper *L. griseus* (Fischer et al. 2003), and canary rockfish *Sebastes pinniger* (Piner et al. 2005; Andrews et al. 2007). Semimarine species include black drum *Pogonias cromis* of the Chesapeake Bay region (Campana and Jones 1998), which reside in estuarine waters during their first year, and Arctic char *Salvelinus alpinus*, which is an anadromous species (Campana et al. 2008). The only entirely freshwater species that have been assayed using this approach are lake trout *S. namaycush* (Campana et al. 2008) and lake sturgeon (Bruch et al. 2009, this issue).

The objectives of this study were to (1) validate the age of freshwater drum with bomb radiocarbon analysis of sagittal otolith cores and evaluate the accuracy of the otolith age estimates; (2) support the age validation with corroboratory evidence on drum year-class strength; and (3) evaluate the accuracy of age estimates derived from freshwater drum scales, anal spines, and dorsal spines.

Methods

Study site.—Lake Winnebago, at 55,728 ha, is the largest inland lake in Wisconsin (WDNR 2004), with a maximum depth of 6.4 m and an average depth of 4.7 m. It is part of the eutrophic Winnebago–Upper Fox–Wolf watershed and is connected to the Great Lakes at Green Bay by the lower Fox River. Of the 76 species of fish found in the Winnebago system, freshwater drum have historically been estimated to consistently have the highest biomass (Priegel 1967; Staggs and Otis 1996).

Sampling.—We sampled freshwater drum captured during Lake Winnebago assessment trawling in October of 1986 and 2003–2007, during Winnebago system fishing tournaments in July 2003 and 2006, and following underwater blasting events as part of a bridge construction project on the Fox River between Lakes Winnebago and Butte des Morts in April 2007. Trawling was conducted during daylight hours in August, September, and October with a 7.9-m-headrope bottom trawl with a 3.8-cm stretch-mesh body and a 1.3-cm stretch-mesh cod end liner. The trawl was towed at 6.4–7.2 km/h for 5 min in each of four to seven randomly selected 1′-latitude × 1′-longitude sampling grids within each of five Lake Winnebago sampling areas.

Otoliths were collected from trawl-captured freshwater drum in stratified-random subsamples in 1986 and 2003–2006 (15 per 25.4-mm length interval), from random subsamples in 2007 (standard volume per cast), from drum greater than 457 mm during fishing tournaments in 2003 and 2006, and from all drum collected following underwater blasting in 2007. Scales were collected in 1986 and from trawl sampling in 2003. Dorsal and anal spines were collected from trawl sampling in 2003. Scales were removed from midway between the lateral line and the mid-base of the spiny dorsal fin, and the second spines of the dorsal and anal fins were cut at their bases using surgical nail nippers. All drum sampled were measured to the nearest 2.5 mm total length (TL) and weighed to the nearest gram. Sex and maturity were discerned for all trawl-sampled drum in 2007. Fish with oocyte or general testes development were considered mature.

Otoliths were washed to remove all adhering tissues and prepared for sectioning by being embedded in EpoKwick fast-cure epoxy resin to prevent fracturing while being cut. Two to four transverse sections, 0.25–0.48 mm thick, were cut through the core of each otolith with an Isomet low-speed diamond blade saw and mounted on glass microscopy slides with cyanoacrylate glue for viewing and storage. Spines were cleaned to remove excess soft tissue, and a 0.25–0.48-mm section was cut with the saw through the basal portion of each. Otolith and spine sections were examined through an Olympus SZX7 dissection microscope equipped with an Olympus DP71 camera using a combination of transmitted and reflected light after either mineral oil or ethanol was applied for clarification. Opaque zones were considered the boundaries of annual growth increments (Casselman 1987). Scales were soaked in water, cleaned with a brush, and viewed on a microfiche projector at 40× magnification. Annual growth increments on scales were defined as continuous opaque zones.

Age validation using bomb radiocarbon dating.— Eighteen otoliths were selected from specimens taken during 1986 and from 2003 to 2006 with an estimated year of core formation between 1948 and 1980 to measure radiocarbon values from before, during, and after the bomb-testing era. One otolith of the original pair was processed for age estimation as described previously and the second otolith was sectioned, aged, and micromilled after being embedded in a hard epoxy (Araldite epoxy GY502 and hardener HY956 in a 5:1 weight ratio). Three adjacent 1-mm-thick transverse sections through the core of the second otolith were cut using multiple blades on an Isomet low-speed diamond blade saw and lightly polished to improve clarity. The growth increment sequence was examined and digitally photographed at 16–40× magnification with reflected light, at a resolution of 2,048 × 2,048 pixels, and then digitally enhanced with Adobe Photoshop CS2 to improve contrast. Age estimates were based on the enhanced images, and aging precision was quantified with coefficient of variation (CV = 100 × SD/mean; Campana 2001).

Otolith cores representing what was assumed to be the first year of life were isolated from the central section of each otolith as a solid piece with a Merchantek computer-controlled micromilling machine with 300-μm-diameter steel cutting bits and burrs. The assumed date of core sample formation was calculated as the year of fish collection minus the number of growth increments between the otolith edge and one-half way along the growth axis of the extracted core. After sonification in Super Q water and drying, the sample was weighed to the nearest 0.1 mg in preparation for ^{14}C assay with accelerator mass spectrometry (AMS). The AMS assays also provided δ^{13}C (‰) values, which were used to correct for isotopic fractionation effects. Radiocarbon values were subsequently reported as Δ^{14}C, which is the per mille (‰) deviation of the sample from the radiocarbon concentration of 19th-century wood, corrected for sample decay before 1950 according to methods outlined by Stuiver and Polach (1977).

The feature of a bomb radiocarbon chronology that is most stable across locations and environments (and thus most useful as a dated marker) is the year of initial increase above prebomb levels in response to the period of atmospheric testing of nuclear weapons. Campana et al. (2008) demonstrated that a Δ^{14}C value 10% above the prebomb background is a robust and accurate indicator of the year of initial appearance of bomb Δ^{14}C, and one that is consistent with atmospheric sources. Therefore, we estimated the value corresponding to the 10% threshold contribution of Δ^{14}C (C_T) by calculating 90% of the range in Δ^{14}C between its lowest (C_L) and peak (C_P) values and subtracting it from the peak value, that is,

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

where C_L occurs on or after 1952, the year of initial release of bomb radiocarbon into the atmosphere. The year of initial appearance of bomb Δ^{14}C (Y_T) is then defined as the year in which the Δ^{14}C chronology first exceeds C_T. To further substantiate the calculated year

TABLE 1.—Collection year, core weight, age (based on otolith growth increments), year-class (based on otolith age), and $\Delta^{14}C$ and $\delta^{13}C$ assay values for freshwater drum sagittal otolith cores sampled from Lake Winnebago, Wisconsin, in 1986, 2003, and 2006.

Collection year	Core weight (mg)	Age	Year-class	$\Delta^{14}C$ (‰)	$\delta^{13}C$ (‰)[a]
2006	11.64	52	1954	−117.1	−9.7
2003	27.42	49	1954	−116.8	−10.2
1986	8.81	31	1955	−124.0	−11.7
	5.87	29	1957	−82.7	−10.1
	5.11	29	1957	−42.7	−8.2
	7.82	27	1959	−38.9	−9.7
	6.82	26	1960	113.2	−8.7
	7.24	24	1962	121.0	−9.3
	7.52	23	1963	112.4	−9.6
2006	8.37	43	1963	113.5	−8.8
1986	7.18	22	1964	215.9	−9.0
2006	7.39	41	1965	234.2	−10.4
1986	5.76	20	1966	217.1	−12.6
2003	33.39	37	1966	219.8	−12.4
1986	7.04	18	1968	181.4	−10.1
	9.3	17	1969	170.6	−10.4
2003	5.07	29	1974	102.3	[b]
2006	9.01	23	1983	77.6	−12.2

[a] $\delta^{13}C$ was used to correct for isotopic fractionation to derive $\Delta^{14}C$, which is the per mille (‰) deviation from the radiocarbon concentration of 19th-century wood (see text).
[b] Data not available.

of initial rise, a second method by Kerr et al. (2004) was used, whereby the year of initial rise is the year that is significantly greater (±2 SD) than the mean prebomb level.

Age corroboration.—Catch-per-unit-effort (CPUE) indices of the age-0 year-class abundance of freshwater drum were collected from 1962 to 1984 with experimental trawling conducted during daylight hours from June to November with a 3.7-m-headrope bottom trawl with a 3.8-cm stretch-mesh body and a 0.65-cm stretch-mesh cod end liner towed at 6.4–7.2 km/h for 7 min in various locations, primarily along the west shore of Lake Winnebago. The average CPUE (number of age-0 freshwater drum per trawl cast) was calculated for each year by averaging the CPUEs over all casts during the months from August to October, and this was used to document strong hatches of drum that might show up in trawl-caught age frequencies during subsequent years.

Age frequencies based on otolith age estimates of freshwater drum caught in assessment trawls on Lake Winnebago were calculated from pooled data in 1986 and 2003–2007 and examined for progressions of strong year-classes over the 21-year period.

Aging accuracy of alternative structures.—Two experienced readers independently estimated the age of each fish by counting the number of visible growth increments on the scales and otolith sections; one experienced reader examined spine sections. Coefficients of variation were calculated for scales and otoliths between the two readers to examine the degree of agreement.

Results

Age Estimation

We collected pairs of sagittal otoliths from 1,361 freshwater drum—1,170 (287 in 1986, 154 in 2003, 127 in 2004, 107 in 2005, 110 in 2006, and 385 in 2007) captured during trawling on Lake Winnebago, 121 obtained from fishing tournaments in 2003 and 2006, and 70 collected following underwater blasting events in 2007. From the 1,361 pairs of otoliths collected, we estimated ages for 1,351 freshwater drum ranging from age 0 (61 mm) to age 58 (599 mm). Male drum began to mature at age 2 (226 mm), and female drum began to mature at age 5 (272 mm). Ten otoliths were not readable due to faulty sectioning, and one otolith was rejected due to a structural deformity making the growth increments indistinct. Growth increments on otoliths were clear and easily interpretable. The between-reader CV was 0.7%.

Age Validation

Micromilling removed the first 1 to 3 years growth of the freshwater drum otolith cores, which provided adequate sample masses for AMS assays ranging from 5.1 to 33.4 mg. Bomb radiocarbon values of otolith cores (as $\Delta^{14}C$) ranged from −124.0 to 234.2 producing a classic $\Delta^{14}C$ curve that correlated well with known ^{14}C reference chronologies (Table 1;

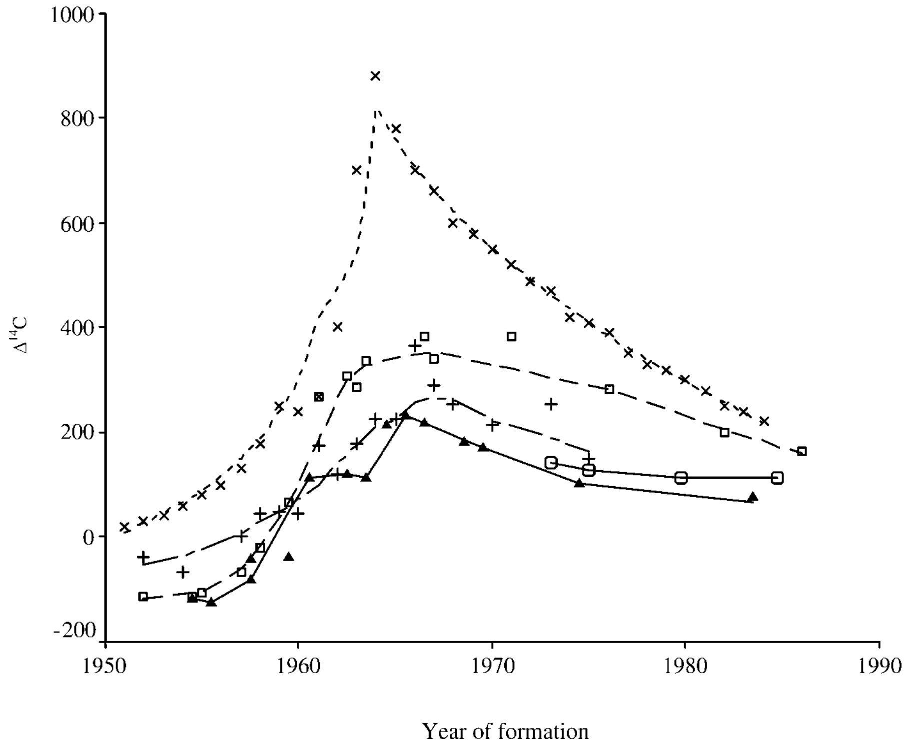

FIGURE 1.—Otolith core $\Delta^{14}C$ chronologies for freshwater drum (triangles), Arctic char and lake trout (small squares; Campana et al. 2008), black drum from Chesapeake Bay (plus signs; Campana and Jones 1998), gray snapper from the Gulf of Mexico (large squares; adapted from Fischer et al. 2003), together with the atmospheric values from the Western Hemisphere (times signs; adapted from Nydal 1993). The $\Delta^{14}C$ values are fitted with locally weighted least-square regressions.

Figure 1). Bomb radiocarbon $\Delta^{14}C$ values showed a sharp increase beginning in 1957, a peak value of 234.2 in 1965, and a steady decline to the most recent sample of 1983. Based on the equation by Campana et al. (2008), 1957 was the initial year of increase in $\Delta^{14}C$ above prebomb levels in the Lake Winnebago freshwater drum chronology. Using the methods of Kerr et al. (2004), the initial year of increase above the mean prebomb level was 1956. Since consistent under- or overaging of the freshwater drum otolith growth sequences would have phase-shifted the entire freshwater drum bomb chronology to the right or left, the close correspondence of the freshwater drum and reference chronologies, and the similarities in their calculated initial years of increase, indicate that the freshwater drum otolith growth increments provide accurate estimates of age. Estimated otolith ages of the drum sampled for ^{14}C ranged from 17 to 52 years. The between-reader CV of the age estimates for the 18 otoliths assayed was 1.72%. The mean SD of the individual radiocarbon assays was approximately 5‰.

Age Corroboration

Examination of freshwater drum year-class strength from experimental trawling samples of age-0 fish from 1962 to 1984 showed a very strong year-class in 1983 (Figure 2). This strong year-class was consistently and clearly the most abundant for each sampling year in 1986 and 2003–2007 based on otolith age estimates (Figure 3). The interpretation of Figures 2 and 3 thus corroborates otolith age estimates up to age 24, since this age-class was still abundant in the 2007 survey year.

Aging Accuracy of Alternative Structures

Growth increments could be seen on scales and the basal sections of anal and dorsal spines, although they were not as clearly distinguishable as those on otoliths (Figure 4). In addition, the lumen of both anal and dorsal spines was often deteriorated, particularly on specimens taken from older individuals.

Age bias plots revealed similar relationships between otoliths and scales, anal spines, and dorsal spines (Figure 5). The age estimates from otoliths begin to

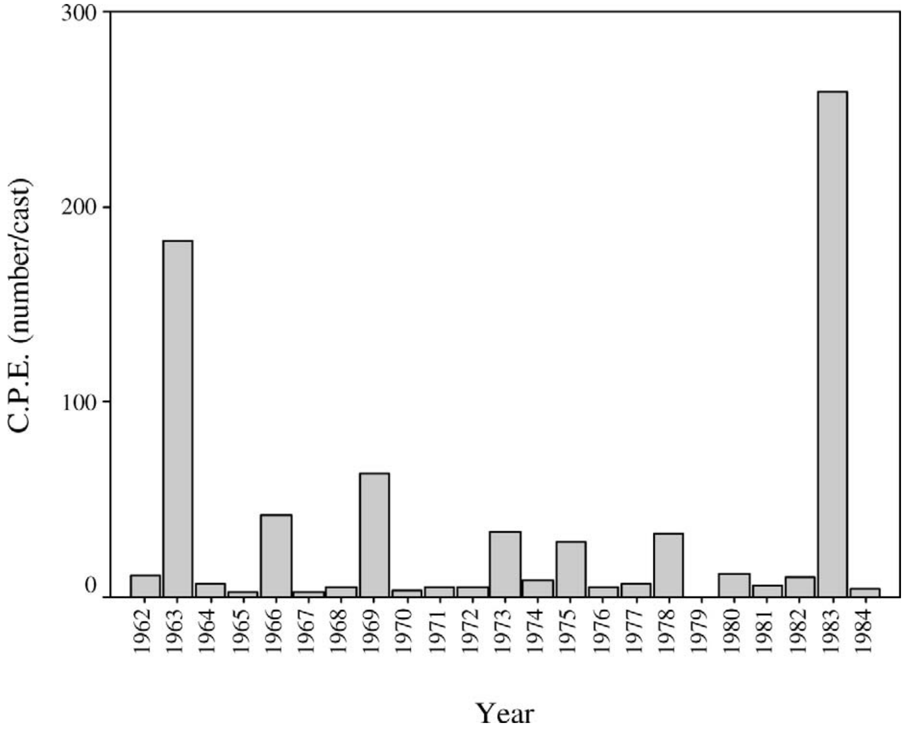

FIGURE 2.—Catch per unit effort (C.P.E.) of age-0 freshwater drum from experimental trawl assessments, Lake Winnebago, 1962–1984.

exceed estimates from the three other structures starting at a length of about 280 mm (age 3). After this point, the otolith age estimates continue to diverge from the scale age estimates by as much as 36 years. The average CV between otoliths and scales was 43.3%, that between otoliths and anal spines 46.5%, and that between otoliths and dorsal spines 49.0%. Log_{10}-transformed otolith ages and log_{10}-transformed scale ages were significantly correlated ($r^2 = 0.71$, $P < 0.00001$, $n = 475$) in a linear regression, although when only data from fish 10 years and older were used in a regression, much less of the variance was explained ($r^2 = 0.23$, $P < 0.00001$, $n = 267$). The two correlation coefficients were significantly different ($Z = 9.45$, $P < 0.0001$) using the statistical test recommended by Zar (1996).

Discussion

The onset and peak of the freshwater drum $\Delta^{14}C$ chronology for Lake Winnebago closely reflects other published $\Delta^{14}C$ values for freshwater and marine fish species, thus validating otoliths as an accurate aging structure to 52 years with an error of no more than ±2 years. Compared with the known-age chronology from Canadian Arctic char and lake trout (Campana et al. 2008), the freshwater drum chronology begins to increase the same year, and peak values occur within 2 years of each other. The black drum chronology from Chesapeake Bay (Campana and Jones 1998) is the most similar to that of the freshwater drum, with an identical initial year of increase of the $\Delta^{14}C$ value 10% above the prebomb background and a slightly lagged peak. The peak freshwater drum $\Delta^{14}C$ values lag slightly behind the atmospheric chronology (Nydal 1993), which would be expected. During the years after the peak, the freshwater drum $\Delta^{14}C$ values are at levels quite similar to those of the gray snapper from the Gulf of Mexico (Fischer et al. 2005).

There are several factors that can affect the timing of the peak value and shape of bomb radiocarbon curves. Peak $\Delta^{14}C$ values often lag slightly behind the atmospheric values due to the time lag between geographic distribution and incorporation of carbon into living tissue (Nydal 1993). For this same reason, $\Delta^{14}C$ values often vary slightly with geographical locations (e.g., Kerr et al. 2004). The water-mixing time tends to be lower in marine systems (e.g., Campana and Jones 1998), and the trophic position or origin of diet items of the organism (e.g., Campana et al. 2002) may cause a lag in the onset of the curve

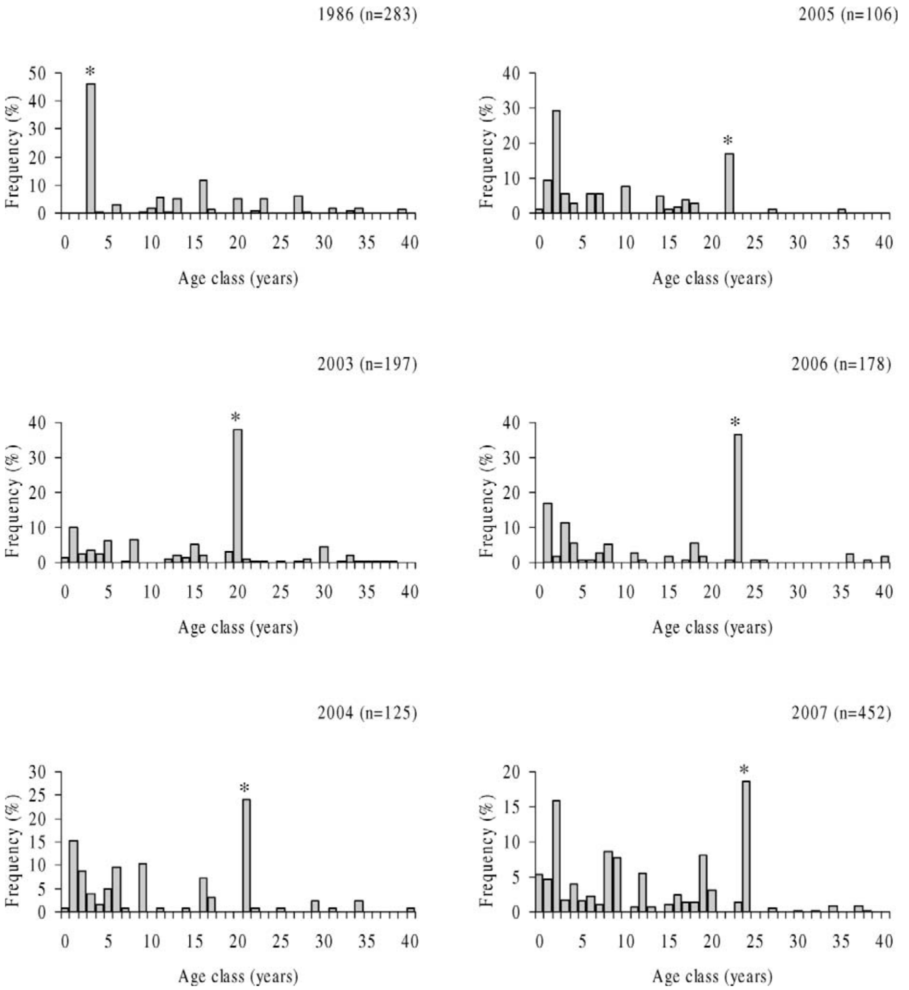

FIGURE 3.—Age frequency histograms for freshwater drum sampled in assessment trawl surveys in 1986 and from 2003 to 2007 at Lake Winnebago showing the progression of the strong 1983 year-class (asterisks). Fish older than age 40 were omitted because of the small sample size.

and differences in $\Delta^{14}C$ values. Large differences in the magnitude of the peak and the postbomb radiocarbon values can reflect regional differences in water mixing rates, which can dilute the bomb signal. Some imprecision in the otolith-coring technique also can affect the shape of the radiocarbon curve.

Freshwater drum otoliths were noted to contain clear periodic increments in the early 1980s (Becker 1983), but at the time these were not validated as annual increments. Goeman et al. (1984) reported age validation of Mississippi River freshwater drum otoliths by following the progression of strong year-classes for three consecutive years. While their study provided strong evidence that freshwater drum otoliths produced accurate ages, the method they used was actually age corroboration, not age validation (Campana 2001). Additionally, in the Goeman et al. (1984) study the progression of strong year-classes did not have consistent representation each year, there were no fish over age 10 in the age frequency histograms, and the overall rigor of the study is unknown because the number of fish plotted on the age frequency histograms is not reported. We consistently identified the strong 1983 year-class of drum in Lake Winnebago in age frequencies using otolith age estimates of drum captured in assessment trawling in 1986 and 2003–2007. The 1983 year-class was first detected in experimental trawl samples as age-0 fish, and persisted in otolith age frequencies in assessment trawl sampling in 1986 and 2003–2007. This year-class progression

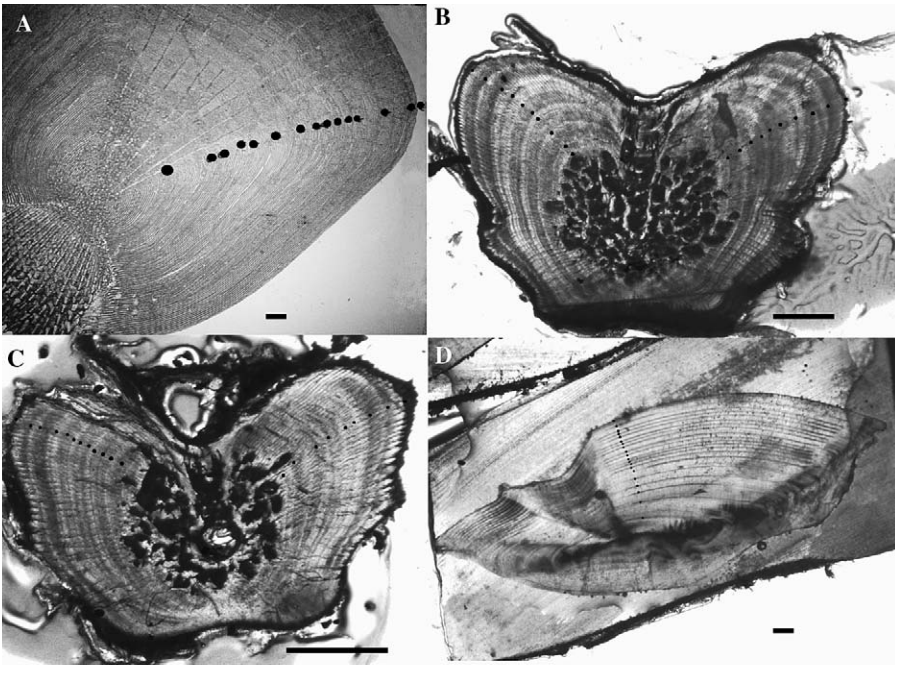

FIGURE 4.—Growth increments of four structures from a 564-mm, 2,268-g freshwater drum from Lake Winnebago in 2003 (sex not determined) yielding different age estimates: **(A)** scale (14 years), **(B)** anal spine (10 years), **(C)** dorsal spine (12 years), and **(D)** transversely sectioned otolith (20 years). The bars represent 1 mm; the black circles indicate the approximate locations of the interpreted annuli. Edges were not counted as complete annuli. If unequal numbers of annuli were counted on the two sides of a spine, the side with the higher number was used.

corroborates the age validation of the older drum assayed for ^{14}C and also supports the accuracy of the age estimates from otoliths of freshwater drum of younger ages.

Published studies on life history characteristics of freshwater drum before 1994 were based on scale age estimates (e.g., Butler and Smith 1950; Daiber 1953; Edsall 1967). After 1994, published studies were primarily based on otolith age estimates (e.g., Pereira et al. 1994, 1995; Rypel et al. 2006; Rypel 2007), although some (e.g., French and Bur 1996; Braaten and Guy 2004) still relied on scale age estimates, perhaps because freshwater drum otoliths had never been truly validated and because virtually all reference books (e.g., Becker 1983; Schultz 2004; Werner 2004) cited age estimates from scales. Von Bertalanffy parameters and sexual dimorphism in growth rates (Palmer et al. 1995), and age-at-maturation parameters (Rypel 2007) based on drum otolith ages have been reported, but without validation of otolith growth increments.

Since our results show that scale ages are inaccurate, all demographic parameters based on scale ages must be incorrect. One effect of this inaccuracy is that changes in parameters, such as mortality and growth rates, cannot be detected over time. We explored the possibility of using the relationship between otolith and scale age estimates from archived scale age data to reconstruct a usable age structure for historic freshwater drum populations. Although we found a significant relationship between scale and otolith age estimates up to age 3, the diminished relationship for structures from older fish reduced the likelihood of accurately discerning true age structure from archived scale age data.

There may be regional or geographical differences in agreement between otolith and scale ages. For Mississippi River freshwater drum, scales were found to overestimate age through age 9 (Goeman et al. 1984). In our study, the TL at which otolith age estimates begin to diverge from scale age estimates corresponds to the TL of the onset maturity of Winnebago freshwater drum. Otolith growth is less likely to be disrupted by maturation than scale growth because otoliths are a vital component of a sensory organ of the nervous system and, unlike scales, otoliths grow throughout the lifetime of a fish and are not subject to resorption (Campana and Neilson 1985). The agreement of spines and scales in our study demon-

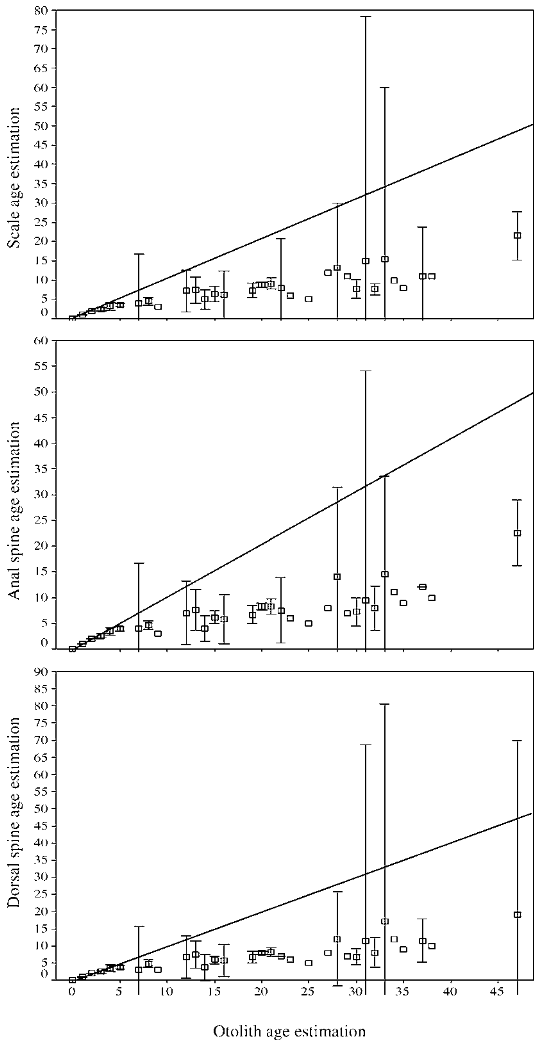

FIGURE 5.—Otolith-estimated ages of freshwater drum from Lake Winnebago in 2003 versus the mean age estimated from scales, anal spines, and dorsal spines. All values are years; the error bars represent 95% confidence intervals. Values that fall on the diagonal lines represent full agreement between the respective structures.

strates that the growth of otoliths is controlled separately from scale and skeletal tissues.

Our validation confirms that the freshwater drum is one of the longest-lived fishes of the Lake Winnebago system, surpassed only by lake sturgeon, which are estimated to attain ages up to 96 years (R. M. Bruch, unpublished data). Other long-lived fishes within the Great Lakes drainage are known to rarely exceed 40 years. Based on otolith age estimates, lake trout in Lake Superior are estimated to live up to 42 years (Schram and Fabrizio 1998), while lake trout in the Arctic were recently validated to live at least 50 years (Campana et al. 2008). Flathead catfish *Pylodictis olivaris* have been reported to attain a maximum age of 17 years in the Lake Michigan drainage based on pectoral spine age estimates (Daugherty and Sutton 2005) and 28 years in the Tallapoosa River, Alabama, based on otolith age estimates (Nash and Irwin 1999). Otolith age estimates show that flathead catfish in the Lake Winnebago system may reach 30 years of age (Allen Niebur, Wisconsin Department of Natural Resources, personal communication). The Great Lakes cisco *Coregonus artedi* was recently reported to reach at least age 18 based on otolith age estimates, much longer than previously thought based on scale age estimates (Yule et al. 2008).

Slow-growing, late-maturing species are more vulnerable to human exploitation (Musick 1999). Early freshwater drum management decisions on the Winnebago system were based on the premise that freshwater drum were a fast-growing, short-lived species with a high mortality rate (Priegel 1967). Our age validation study indicates, however, that freshwater drum live much longer than the majority of other species in the Lake Winnebago fish community and, unlike most other long-lived species (e.g., lake sturgeon), mature at a relatively young age and spawn annually. This strategy optimizes an individual's reproductive value. For example, a female lake sturgeon living to age 80 will spawn an average of 15 times within her lifespan, while a female freshwater drum living to an age of 50 will spawn approximately 45 times in her life span. This unique trait allows freshwater drum to be more prolific than fish species with a late-maturing life history strategy, which may partially explain why freshwater drum are geographically widespread and frequently abundant where present. This life history trait undoubtedly contributed to the poor success of 55 years of rough fish removal programs on Lake Winnebago designed to reduce drum abundance (Priegel 1967; Kamke and Bruch 1991).

Our results support revision of reference books that base the life history characteristics of freshwater drum on scale age estimates. For example, the maximum lifespan reported in Becker (1983), a commonly cited fisheries reference book for fishes from Wisconsin, is 17 years. The maximum age of Lake Winnebago freshwater drum in this study was 58 years based on the validated otolith ages. A freshwater drum sampled from Lake Winnebago in the late 1980s was estimated from otoliths to be age 70 (R.M.B., personal observation). The greatest maximum published age based on otoliths of freshwater drum from the Red Lakes, Minnesota, is 71 years (Pereira et al. 1994). The Red Lakes and Lake Winnebago provide similar habitats, occur within similar latitudes, and are both large, shallow systems with no seasonal thermal stratification. The maximum lifespan of freshwater drum in Alabama based on otolith age estimates was reported to be about 30 years (Rypel et al. 2006). With the validation of ages derived from freshwater drum sagittal otoliths, it is important that all freshwater drum age estimation is based on otoliths, the only structure in drum that provides precise and accurate estimates of age for calculation of meaningful demographic population parameters.

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