

Age estimations of wild pallid sturgeon (*Scaphirhynchus albus*, Forbes & Richardson 1905) based on pectoral fin spines, otoliths and bomb radiocarbon: inferences on recruitment in the dam-fragmented Missouri River

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Summary

An extant stock of wild pallid sturgeon *Scaphirhynchus albus* persists in the fragmented upper Missouri River basin of Montana and North Dakota. Although successful spawning and hatch of embryos has been verified, long-term catch records suggest that recruitment has not occurred for several decades as the extant stock lacks juvenile size classes and is comprised exclusively of large, presumably old individuals. Ages of 11 deceased (death years 1997–2007) wild *S. albus* (136–166 cm fork length) were estimated based on pectoral fin spines, sagittal otoliths and bomb radiocarbon (¹⁴C) assays of otoliths to test the hypothesis that members of this stock are old and to provide inferences on recruitment years that produced the extant stock. Age estimations based on counts of presumed annuli were about 2 years greater for otoliths (mean = 51 years, range = 43–57 years) than spines (mean = 49 years, range = 37–59 years). Based on ¹⁴C assays, confirmed birth years for all individuals occurred prior to 1957, thus establishing known longevity of at least 50 years. Estimated age based on presumed otolith annuli for one *S. albus* was validated to at least age 49. Although ¹⁴C assays confirmed pre-1957 birth years for all *S. albus*, only 56% of estimated ages from spines and 91% of estimated ages from otoliths depicted pre-1957 birth years. Both ageing structures were subject to under-ageing error (up to 15 years). Lack of or severe curtailment of *S. albus* recruitment in the upper Missouri River basin since the mid-1950s closely parallels the 1953–1957 timeframe when a mainstem reservoir was constructed and started to fill. This reservoir may function as a system-wide stressor to diminish recruitment success of *S. albus* in the upper Missouri River basin.

Introduction

The pallid sturgeon (*Scaphirhynchus albus*) is a fluvial specialist (Galat et al., 2005) that inhabits the Missouri River from Montana to its confluence with the Mississippi River near St. Louis, Missouri, the middle and lower reaches of the

Mississippi River, and large tributaries of these river systems (Bailey and Cross, 1954; Kallemeyn, 1983). *Scaphirhynchus albus* was designated as federally endangered in 1990 (USFWS, 1993) owing to declining wild stocks throughout the range of the species and lack of or critically limited spawning and recruitment success. A variety of stressors have been implicated as factors of imperilment for *S. albus* including habitat loss and degradation (e.g. dam construction, altered flow and temperature regimes, river channelization), harvest, pollution and contaminants, and hybridization (USFWS, 1993, 2000, 2014).

A wild stock of adult *S. albus* persists in the upper Missouri River basin of Montana and North Dakota, but the stock is confined to lotic reaches bounded by large mainstem dams and reservoirs on the Missouri River and an irrigation dam on the Yellowstone River. Abundance estimates suggest that the wild stock declined from nearly 1000 individuals in the late 1960s to 100–125 individuals in recent years (Braaten et al., 2009a). Although reproduction by *S. albus* has been documented in this portion of the upper Missouri River basin (Fuller et al., 2008; Fuller and Braaten, 2012; DeLonay et al., 2014; Eichelberger et al., 2014), no recent recruitment has been detected, as the existing wild stock is comprised exclusively of large, presumably old adult individuals (USFWS, 2007). Limited information on ages of wild *S. albus* is available in the upper Missouri River basin to provide inferences on birth years or recruitment events that produced the extant stock. Based on counts of presumed annuli on pectoral spines, Keenlyne and Jenkins (1993) estimated that a 124-cm fork length (FL) male *S. albus* collected from the upper Missouri River basin in 1988 was 37 years old, suggestive of a 1951 birth year. Krentz et al. (2003) also used pectoral spines to estimate ages for seven *S. albus* (136–160 cm FL) from this stock; estimated ages ranged from 31 to 55 years with presumed birth years spanning 1940–1967. These results, in combination with evidence of long-term recruitment failure (USFWS, 2007), present the hypothesis that individuals characteristic of the extant stock of wild *S. albus* in the upper Missouri River basin are old and were produced from spawning events prior to the mid-1960s.

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However, potential under-estimation of ages from sturgeon pectoral spines (i.e. Rien and Beamesderfer, 1994; Paragamian and Beamesderfer, 2003; Bruch et al., 2009) presents the possibility that the extant stock of *S. albus* may have resulted from spawning events prior to the mid-1960s, perhaps pre-dating closure of the last dam in the upper Missouri River basin during the early 1950s.

Inaccuracies of age estimations from sturgeon pectoral spines may confound interpretations of when successful year classes were last produced in this stock. As an alternative to pectoral spines, otoliths have been used to age lake sturgeon *Acipenser fulvescens* and have been shown to be more accurate than pectoral spines (Bruch et al., 2009). In addition, the use of bomb radiocarbon dating techniques has emerged as an effective method to validate or confirm presumed increments, and accurately estimate ages and longevity in long-lived fishes. Atomic bomb detonations during the 1950s and early 1960s caused substantial increases in atmospheric radiocarbon (^{14}C) that were incorporated into the hard parts of fishes (e.g. Kalish, 1993). Fish structures formed prior to about 1957 contained low concentrations of ^{14}C ; whereas, structures after 1957 contained elevated and rapidly increasing ^{14}C concentrations through the 1960s (Campana et al., 2008; Davis-Foust et al., 2009). Assays for ^{14}C have been widely applied in marine (Kalish, 1993; Baker and Wilson, 2001; Campana et al., 2002; Kerr et al., 2004) and freshwater (Campana et al., 2008; Bruch et al., 2009; Davis-Foust et al., 2009) systems to discern pre- or post-bomb birth years, validate ages, and provide estimates of longevity in long-lived species. As in *A. fulvescens* (Bruch et al., 2009), bomb radiocarbon ageing techniques would be expected to be highly applicable to adult *S. albus* from the upper Missouri River basin given assumed birth years spanning the 1940s (pre-bomb years) through the mid-1960s (post-bomb years). Although highly effective for validating the birth year (and hence age) of a fish born between 1957 and 1965, environmental radiocarbon was low and relatively uniform prior to 1957, thus limiting the value of the technique for fish born before 1957.

The goal of this project was to estimate ages and birth years of wild adult *S. albus* in the upper Missouri River basin, thus providing inferences on spawning and recruitment events that produced the extant wild stock. The objectives were to: (i) estimate and compare ages of wild adult *S. albus* based on counts of presumed annuli on pectoral spines and sagittal otoliths, and (ii) validate age estimations based on concurrence between ^{14}C concentrations in otoliths and known concentrations of radiocarbon in freshwater systems.

Materials and methods

Study area

The research sample of *S. albus* examined in this study was comprised of individuals from an extant wild stock (USFWS, 2007) that occupy the Missouri River and Yellowstone River in western North Dakota and eastern Montana (Fig. 1). The Missouri River portion of the study area extends about 325 km from Fort Peck Dam located at river km (rkm) 2850 to the full-pool headwaters (near rkm 2526) of Lake Sakakawea.

Fort Peck Dam was closed in 1937, and Garrison Dam (located at rkm 2238) which impounds Lake Sakakawea was closed in 1953. Gradual filling of Lake Sakakawea occurred from 1954 to 1966, and the reservoir reached full pool in 1967 at an elevation of 565.4 m above sea level (Scarnecchia et al., 1996; Fig. 1). The Missouri River downstream from Fort Peck Dam is hydrologically and thermally altered as dam operations modify the timing and magnitude of discharge regimes (Bowen et al., 2003) and hypolimnetic releases suppress water temperatures (Braaten et al., 2009b). The Yellowstone River study area extends from the confluence at the Missouri River (rkm 2547) 117 rkm upstream to Intake Diversion Dam (Fig. 1). In contrast to the Missouri River, the Yellowstone River maintains relatively natural discharge and thermal regimes owing to the lack of mainstem dams on the system (Bowen et al., 2003).

Research sample of *S. albus* and ageing structures

The research sample of *S. albus* was comprised of 11 wild adults from the study area that died between 1997 and 2007 during activities associated with artificial spawning programs in hatcheries (USFWS, 2008). Ten frozen individuals were housed at the University of Alabama whole-fish repository in Tuscaloosa, Alabama. One frozen individual was maintained at the U. S. Fish and Wildlife Service Garrison Dam National Fish Hatchery in Riverdale, North Dakota. The research sample included eight females (mean FL = 156.0 cm, range = 143–166 cm; mean weight = 26.5 kg, range = 17–31 kg) and three males (mean FL = 147.0 cm, range = 136–159 cm; mean weight = 21.3 kg, range = 15–25 kg). The large sizes of *S. albus* examined in this study were representative of the majority (~80%) of *S. albus* reported in long-term catch records for the upper Missouri River basin (USFWS, 2007), but the research sample did not include representatives of smaller *S. albus* (90–130 cm) caught in the upper basin (USFWS, 2007).

After thawing, a pectoral fin spine was removed at the point of articulation with the fish body and pairs of sagittal otoliths were excised from the neurocranium. Although otoliths were removed from all individuals, pectoral fin spines were obtained for only nine of the 11 *S. albus* as two individuals housed at the whole-fish repository were missing pectoral spines prior to our handling. Pectoral spines were dried for several days, embedded in epoxy, allowed to harden, and at least two 0.5- to 0.6-mm sections were cut distal to the propterygium (Findeis, 1997; Bruch et al., 2009) using an Isomet low-speed saw. Digital images of the pectoral spine sections were captured under transmitted and reflected light, and age was estimated by counting presumed annuli on the digital images.

Otolith processing procedures followed Bruch et al. (2009) with slight modifications. After drying in epoxy, three adjacent 1-mm thick horizontal sections of the otolith from the core to the postrostrum were prepared with a single cut using multiple blades separated by spacers on an Isomet low-speed saw. Viewed under a binocular microscope (10–20 \times magnification) using reflected light, the growth increment sequence of the otolith was digitally photographed at a resolution

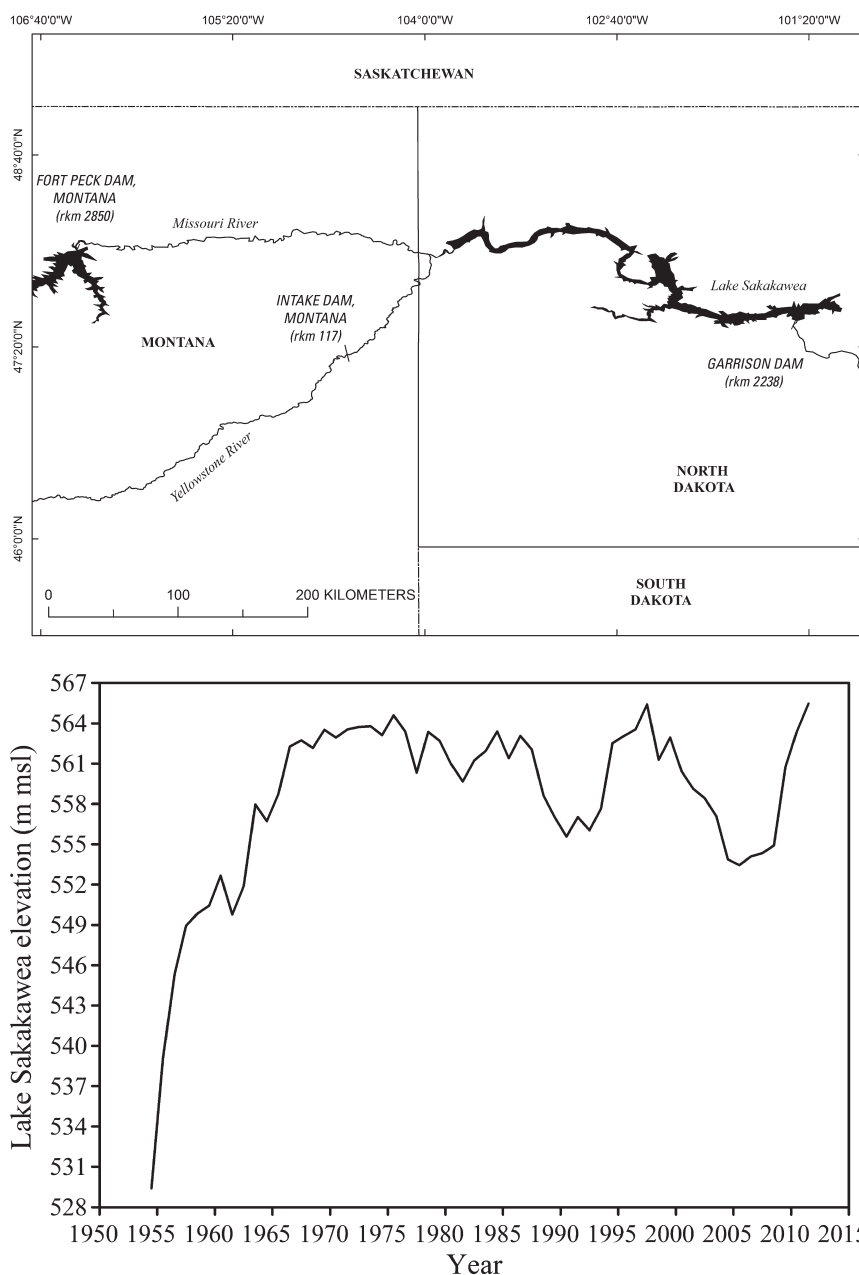


Fig. 1. Study area of the upper Missouri River basin between Fort Peck Dam and Garrison Dam (top panel) and filling chronology of Lake Sakakawea following closure of Garrison Dam in 1953 as depicted by water surface elevations on 1 July by year (bottom panel)

of 4140×3090 pixels, then digitally enhanced for sharpness and clarity using Adobe Photoshop CS2[®]. Ages were estimated by counting presumed annuli on the enhanced images. A paired *t*-test was used to test the hypothesis that the mean difference in estimated age between structures (otolith age minus spine age) differed from zero.

Bomb radiocarbon

Otolith material representing what was assumed to be the first 5–15 years of life (hereafter referred to as the otolith core) was isolated as a solid piece with a Merchantek[™] computer-controlled micromilling machine using 300- μ m diameter steel cutting bits and burrs. In some individuals, core

material was obtained from the right and left otoliths and combined. Occasionally, core material from the same otolith was isolated from two sections adjacent to the central section, but restricted to fewer growth increments so as to allow for the offset of these lateral sections from the primordium. This procedure of obtaining material from both otoliths of the pair, plus occasional multiple sections per otolith, was necessary to maximize the amount of sample material available for assay (2 mg minimum) from each *S. albus*. The presumed year of core sample formation was calculated as year of fish death minus the estimated age span of the fish from the edge of the otolith to the midpoint of the range of growth increments present in the extracted core. This process yielded a mean year of core formation. In addition to otolith

cores, material was also micromilled from the middle growth regions of otoliths in two *S. albus* and assayed separately. Thus, for these two individuals, radiocarbon values could be ascertained for years representing both the early and middle years of the life span. Micromilled samples were weighed to the nearest 0.1 mg in preparation for ^{14}C assay with accelerator mass spectrometry (AMS). The AMS assays also provided $\delta^{13}\text{C}$ (‰) values, which were used to correct for isotopic fractionation effects and provide information on the source of the carbon. Radiocarbon values were subsequently reported as $\Delta^{14}\text{C}$, which is the per-mille (‰) deviation of the sample from the radiocarbon concentration of 19th-century wood, corrected for sample decay prior to 1950 according to methods outlined by Stuiver and Polach (1977). The mean standard deviation of the individual radiocarbon assays was about 5‰.

The year of formation of the *S. albus* otolith core can be estimated by comparing its radiocarbon content with that of a reference radiocarbon chronology based on known-age material. This process yields inferences on the accuracy of age estimations as the mean year of formation of assayed otolith material is based on counts of presumed annuli (e.g. ^{14}C assays would be off-set from the reference chronology if ageing error occurred). Lacking a reference radiocarbon chronology for fishes in the Missouri River, radiocarbon assays for *S. albus* were compared to a reference radiocarbon chronology developed for freshwater drum *Aplodinotus grunniens* sampled in Lake Winnebago, Wisconsin (Davis-Foust et al., 2009). Radiocarbon chronologies do not vary across species and are remarkably uniform in surface freshwater around the world (Campana et al., 2008), so the Wisconsin reference chronology should be closely applicable to Missouri River sturgeon. Although the *A. grunniens* chronology was, strictly speaking, not a chronology based on known-age material, otoliths of *A. grunniens* are well known for their clear and easily-interpreted growth pattern, implying that the date of formation of their cores can be determined with great accuracy (Pereira et al., 1995). Age estimations based on comparison of sample radiocarbon chronologies with the reference chronology are typically accurate to within 1–3 years (Campana, 2001).

Results

Pectoral spines and otoliths from *S. albus* displayed numerous presumed annuli suggesting that individuals were very old (Fig. 2). Duplicate readings of presumed annuli on pectoral spines and otoliths yielded variable age estimates within structures. The difference between duplicate age assignments for pectoral spines averaged 3.2 years (coefficient of variation, $\text{CV} = 4.5\%$), with duplicate readings varying from a minimum of zero (fish number 9, estimated age 37 years) to a maximum of 8 years (fish number 6, 53–61 years, mean age 57 years; Table 1). The difference in age estimates from otolith pairs averaged 4.3 years ($\text{CV} = 5.0\%$), and deviated from a minimum of zero (fish number 5, 52 years) to a maximum of 11 years (fish number 2, 49–60 years, mean age 55 years; Table 1).

The mean difference in paired age estimates from otoliths and pectoral spines did not differ significantly from zero

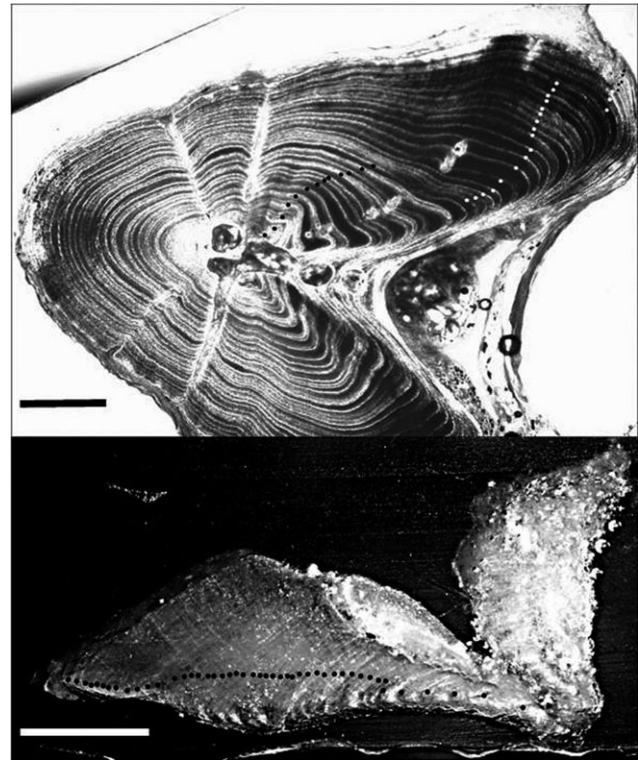


Fig. 2. Transverse thin section of a pectoral spine (top) and otolith (bottom) from a female *S. albus* (163.0 cm, 28.1 kg; death year 2004), image-enhanced and annotated to show presumed annuli. The estimated mean age assigned to the structures was 37 years for the spine and 49 years for the otolith. Scale bar = 1.0 mm for both structures

(paired t -test, $t = 0.98$, $P = 0.36$, mean difference = 2.3 years); mean age was 50.9 years for otoliths (range 43–57 years) and 48.6 years for spines (range 37–59 years; Table 1). Birth year estimates based on presumed ages spanned 1943–1957 (mean = 1951.3) for otoliths and 1943–1967 (mean = 1953.6) for pectoral spines, with the presumed youngest *S. albus* in the data set (birth years 1959–1967) reflecting ages based on pectoral spines. The otolith data set including all 11 *S. albus* yielded a mean age of 50.1 years and mean birth year of 1951.8 (Table 1).

Bomb radiocarbon ($\Delta^{14}\text{C}$) values for otolith cores and increments ranged between -187 and 135 , which is the expected $\Delta^{14}\text{C}$ range for pre-bomb (before 1957; $\Delta^{14}\text{C}$ less than -100) and post-bomb (after 1961; $\Delta^{14}\text{C}$ greater than 0) otolith material (Table 1). Otolith cores for eight *S. albus* (fish numbers 1, 2, 3, 4, 5, 6, 8, 11) had highly depleted $\Delta^{14}\text{C}$ values (-187.4 to -131.2) indicating that the otolith cores from these fish were produced prior to 1957 (Fig. 3; Table 1). For these eight *S. albus*, birth year estimates from otolith annuli and mean year of core formation tended to agree with the pre-1957 birth year assignment based on ^{14}C assays; however, evidence for otolith under-aging existed in three fish. For fish number 1 and 3, the mean year of core formation based on otolith annuli and corresponding highly depleted $\Delta^{14}\text{C}$ values were inconsistent with the *A. grunniens* radiocarbon chronology (Fig. 3). Otolith ages were nominally

Table 1

Fish numbers, fork length, sex, death year, mean age as estimated from annual increment counts on pectoral spines and otoliths, estimated birth year based on mean age from pectoral spines and otoliths, mean estimated year of ^{14}C -assayed otolith core increments (based on otolith ages), and $\Delta^{14}\text{C}$ value for *Scaphirhynchus albus* from the upper Missouri River basin

Fish number	Sex	Length (cm)	Death year	Spine age (years)	Birth year from spine age	Otolith age (years)	Birth year from otolith age	Mean year of otolith core formation	$\Delta^{14}\text{C}$ value (‰)
1	♀	164.2	1997			43	1954	1958.9	-159.4
2	♀	145.9	1998	46	1952	55	1943	1949.2	-138.5
3	♀	142.5	2000	50	1950	43	1957	1963.2	-131.2
4	♂	159.4	2002	59	1943	52	1950	1956.0	-156.2
5	♀	157.0	2002	52	1950	52	1950	1955.5	-164.8
6	♂	145.0	2002	57	1945	53	1949	1952.8	-164.3
7	♀	143.5	2002	42	1960	47	1955	1962.9	81.0
8	♀	165.7	2003	46	1957	50	1953	1960.4	-162.0
								1973.0 ^a	-150.5
9	♀	163.0	2004	37	1967	49	1955	1958.0	-26.5
10	♀	166.0	2004			50	1954	1961.0	-79.7
								1975.5 ^a	135.1
11	♂	136.0	2007	48	1959	57	1950	1955.4	-187.4

^aEstimated mean year of increment formation for middle growth regions of the otolith.

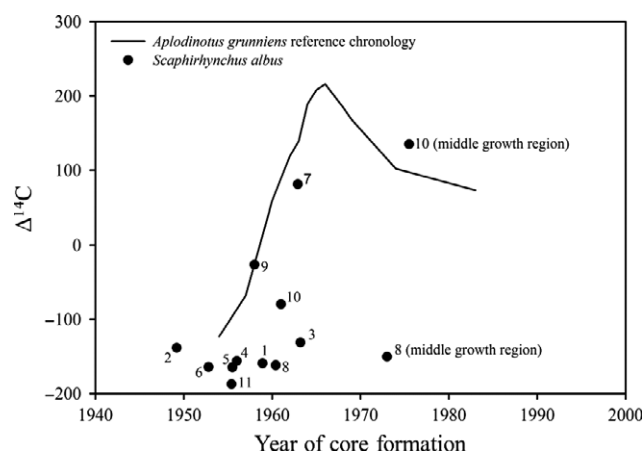


Fig. 3. Radiocarbon values (reported as $\Delta^{14}\text{C}$, ‰) for *S. albus* core and outer increment otolith assays depicting mean year of formation based on estimated ages (solid dots; numbers correspond to individual fish in Table 1). The *A. grunniens* $\Delta^{14}\text{C}$ reference chronology adapted from Davis-Foust et al. (2009) is also presented as a solid line fit using a loess procedure

underestimated by 2 years (fish 1) to 6 years (fish 3). Evidence of extreme under-aging of otoliths was detected for fish number 8 as $\Delta^{14}\text{C}$ values for the core (-162.0; presumed mean year of formation = 1960.4) and middle growth regions (-150.5; presumed mean year = 1973.0) were clearly representative of pre-1957 $\Delta^{14}\text{C}$ values; the otolith age of this individual was nominally underestimated by 15 years (Fig. 3). The highly depleted $\Delta^{14}\text{C}$ values validated pre-1957 birth year estimates from pectoral spine ages except in two cases (fish number 8, estimated spine birth year 1957, estimated otolith birth year 1953; fish number 11, estimated spine birth year 1959, estimated otolith birth year 1950; Table 1).

In contrast to the eight *S. albus* with highly depleted $\Delta^{14}\text{C}$ values, core assays for three individuals (fish numbers 7, 9, 10) and the assay of outer growth regions for fish number 10 were less depleted ($\Delta^{14}\text{C}$ values -26.5 to 135.1; Table 1) and

closely corresponded to the ascending and descending limbs of the *A. grunniens* radiocarbon chronology (Fig. 3). A such, these individuals provided additional inferences on age estimates based on counts of presumed annuli on aging structures. Specifically, otolith core assays for fish 9 (presumed mean core year = 1958.0) closely corresponded to the initial ^{14}C increase suggesting that this individual was accurately aged at 49 years old based on presumed otolith increments with an estimated birth year of 1955 (Fig. 3). The estimated spine age for fish 9 was 37 years old with an estimated birth year of 1967, a year which is inconsistent with the $\Delta^{14}\text{C}$ value and thus indicates spine under-aging by at least 10 years. Core assays for fish 7 (presumed mean core year = 1962.9), fish 10 (presumed mean core year = 1961) and the increment assay for fish 10 (presumed mean increment year 1975.5) were slightly phase-shifted from the *A. grunniens* radiocarbon chronology (Fig. 3) indicating that these fish were slightly under-aged using otoliths by 2 years (fish 7) and 4–5 years (fish 10). Thus, fish 7 was likely produced in 1953 (49 years old) and fish 10 in 1949–1950 (54–55 years old). The estimated birth year for fish 7 based on spines was 1960 (42 years), thus the spine age was underestimated by 7 years. Comparative spine age for fish 10 was not available as spines were not available for this fish.

Discussion

The large body size of *S. albus* examined in this study combined with the apparent lack of wild recruitment in the upper Missouri River basin (USFWS, 2007) established the working hypothesis that the extant stock of wild adults, from which the research sample of *S. albus* in this study was obtained, was potentially very old. Serving as a known date marker in the environment, the bomb radiocarbon chronology provided the template to examine this hypothesis and discern the reliability of presumed annuli on spines and otoliths as true indicators of age. Otolith radiocarbon assays and otolith-based ages established that all *S. albus* examined

in this study were produced prior to 1957; however, definitive birth years could not be identified as bomb radiocarbon in freshwater is a year-specific marker back to about only 1957 (Bruch et al., 2009) and otolith ages for all individuals extended to pre-1957 birth years.

Due to the old age of *S. albus* that were assayed, validation of presumed annuli on spines and otoliths as accurate age indicators could not be assessed in the majority of the *S. albus* examined. In this regard, it is unfortunate that more samples with birth years in the early and mid-1960s during the period of increasing ^{14}C values were not available as these samples would have been the most useful for confirming and validating age relative to the *A. grunniens* radiocarbon chronology. Nonetheless, the results provided strong inferences on the accuracy of ageing old *S. albus* using otoliths and spines, and provided accurate and indisputable minimum ages. Close correspondence between the otolith age of fish number 9 and the *A. grunniens* radiocarbon chronology provides evidence that this individual was accurately aged to at least 49 years old using otolith annuli. The slight phase-shift of otolith ages for fish number 7 and fish number 10 relative to the *A. grunniens* radiocarbon chronology similarly suggests that these individuals were aged relatively accurately. However, counts of presumed annuli on otoliths also tended to underestimate age for several individuals. Although an annulus probably forms each year on otoliths of *S. albus* from the upper Missouri River basin, counts of annuli are subject to random error, as they are in any species (Campana, 2001). Indeed, annuli on otoliths of *S. albus* were often difficult to discern relative to other species. Bruch et al. (2009) validated otolith annulus formation in *A. fulvescens* based on bomb radiocarbon, and similar to our study, they found otolith annuli were valid to about age 52 years. In comparison to otoliths, age estimates from five (56%) *S. albus* spines were validated to pre-1957 concordant with age determinations from the radiocarbon chronology. Ages from three (33%) spines were nominally under-aged by 1–3 years based on the radiocarbon chronology. These results lend support to the presumption that pectoral spine increments in *S. albus* from the upper Missouri River basin can represent true annuli; however, the potential for under-aging also exists for this structure as evidenced by the finding that the spine age from the one remaining *S. albus* (fish number 9) was nominally under-aged by 10 years based on the radiocarbon chronology. Initial attempts to validate pectoral spine ages of *S. albus* have focused on young known-age hatchery stocks. Hurley et al. (2004) reported that only 28% of the spine age estimates reflected known-age for age-6 *S. albus* confined to a hatchery environment, and also indicated that they tended to underestimate ages of the young *S. albus*. Koch et al. (2011) reported that true age was verified in 28% of spines from known-age (age-1 to age-7) hatchery-produced *S. albus* released and recaptured in the Missouri River. Killgore et al. (2007) reported that the number of pectoral spine annuli on a hatchery-raised and released juvenile *S. albus* collected in the Mississippi River agreed with the known-age (5 years). In other sturgeons, spine annuli may be accurate indicators of age for younger individuals but accuracy tends to diminish with increasing longevity (Rien and Beamesder-

fer, 1994; Rossiter et al., 1995; Paragamian and Beamesderfer, 2003; Bruch et al., 2009).

Differences in age estimates between paired spine and otolith readings ranged from 0 to 12 years across the sample of old *S. albus* examined in this study, and although the mean difference was not significantly different from zero, otoliths yielded a slightly greater age (2.3 years) than spines. However, despite the relatively high level of ageing precision within both structures (4.5–5.0%), spines and otoliths were subject to ageing error that resulted in underestimates of age for several individuals based on the $\Delta^{14}\text{C}$ values and the radiocarbon chronology. In addition, it is possible that some spine or otolith ages may have been overestimated, but detection of this error was not possible because pre-bomb radiocarbon levels in reference chronologies remain relatively constant prior to 1957. In their comparison of *A. fulvescens* otoliths and spines across a broad range of ages, Bruch et al. (2009) found that spine ages were less than otolith ages beyond age-14 years, and that spines under-estimated true age by 10–15 years in *A. fulvescens* 40–60 years old. Although pectoral spines and otoliths can be used to age sturgeons, spines will likely remain the primary ageing structure for *S. albus* due to the endangered status of the species and necessity of sacrificing individuals to obtain otoliths. However, mortalities of *S. albus* that occur during field studies also facilitate acquisition of otoliths, and as indicated in this study, otoliths can improve accuracy of estimations. For example, the age of fish number 9 was definitively under-estimated from spines (37 years); whereas, the otolith age (49 years) was accurate and closely agreed with the radiocarbon chronology. Acquisition of both structures from mortalities provides additional opportunity to compare and validate spine and otolith ages given that age validation using spines has met with limited success (Hurley et al., 2004; Koch et al., 2011).

With birth years pre-dating 1957, the research sample of *S. albus* in this study exhibited a minimum longevity (death year minus 1957) varying from 40 years (fish number 1, death year 1997) to 50 years (fish number 11, death year 2007). However, under-aging of fish number 8 by at least 15 years as evidenced from the highly depleted ^{14}C values suggests that this female was nominally 65 years old prior to death in 2003. Limited accounts of ages for wild *S. albus* exist throughout the species range, and prior inferences on longevity have been based on unvalidated ages from pectoral spines. Maximum ages of 17–21 years have been reported for *S. albus* in the lower Mississippi and Atchafalaya river systems (Keenlyne and Jenkins, 1993; Killgore et al., 2007) and at least 14 years for *S. albus* in the middle Mississippi River (Killgore et al., 2007). Carlson and Pflieger (1981) reported that *S. albus* in the lower Missouri River and Mississippi River attained an age of at least 14 years based on age estimates from a limited sample of individuals. *Scaphirhynchus albus* from Missouri River impoundments in South Dakota have been aged to 25–27 years old (Kallemeyn, 1983; Keenlyne and Jenkins, 1993), and individuals from the Missouri River in North Dakota have been estimated to be 31–55 years old (Keenlyne et al., 1992; Keenlyne and Jenkins, 1993; Krentz et al., 2003). These spine-based estimates of age

from throughout the species range, in comparison to spine ages in the present study, suggest that *S. albus* may exhibit a latitudinal gradient in longevity as maximum age tends to increase from southern to northern portions of the species range. Unfortunately, this trend could not be tested for otolith-based ages as otoliths were not examined in earlier investigations.

The wild stock of *S. albus* in the Missouri River and Yellowstone River reaches of the upper Missouri River basin has declined from an estimated 1000 adults in the 1960s to an estimated 100–125 adults in recent years (Braaten et al., 2009a). This stock has also experienced either prolonged recruitment failure or severely limited recruitment based on size composition from long-term catch records (USFWS, 2007, 2014). However, uncertainty exists regarding the timeframe when recruitment ceased or was severely curtailed. Representing lengths characteristic of about 80% of the extant stock (>130 cm; USFWS, 2007), the research sample of *S. albus* examined in this study (136–166 cm) expressed definitive pre-1957 spawning and recruitment years based on radiocarbon assays. Thus, results suggest that the majority of *S. albus* in the extant stock originated from spawning and recruitment events prior to the mid-1950s. Ages were not assessed for smaller *S. albus* in the extant stock (90–130 cm, representing about 20% of the extant stock; USFWS, 2007) due to the unavailability of ageing structures from deceased individuals. Lacking inferences on age for the smaller individuals, it is unknown if these *S. albus* from the extant stock originated from pre- or post-1957 spawning and recruitment events. However, low representation of smaller individuals in the extant stock combined with the documented complete lack of juvenile size groups (USFWS, 2007) suggests that recruitment has been drastically reduced since the mid-1950s. Stressors contributing to the lack of or diminished recruitment success have been proposed, but differ between the Missouri River and Yellowstone River. For example, the construction of Fort Peck Dam in 1937 and corresponding hypolimnetic flow regulation from the dam have been implicated to diminish suitability of the Missouri River for spawning *S. albus* (USFWS, 1993, 2000, 2014). For the Yellowstone River, lack of recruitment has been attributed to construction in 1905 of a river-wide irrigation dam that fragments migration corridors and disrupts reproductive processes (USFWS, 1993, 2003, 2014; USBOR, 2010). Whereas stressors on the Missouri River and Yellowstone River have affected spawning and recruitment potential, evidence from the present study indicates successful spawning and recruitment of *S. albus* occurred between completion of these projects in 1905–1937 and the mid-1950s when the most recent year classes of *S. albus* examined in this study were produced. However, it is unknown whether recruits during the interim years originated from the Missouri River, Yellowstone River or both river systems.

Although some recruitment by *S. albus* in the upper Missouri River basin occurred through mid-1950s as evidenced from the radiocarbon assays, study results combined with lack of wild-produced juvenile fish in recent decades (USFWS, 2007) establishes the hypothesis that recruitment ceased or was severely curtailed after the mid-1950s to sug-

gest that a system-wide stressor equally affecting the Missouri River and Yellowstone River diminished recruitment potential from both rivers after about 1957. The completion of Garrison Dam in 1953 and initiation of filling of Lake Sakakawea during the mid-1950s correspond to this timeframe. Based on known life history requirements of *S. albus* and hypothesized effects of reservoir conditions on survival, evidence suggests that recruitment success in the upper Missouri River basin was affected by the transition of the system from a free-flowing river to a reservoir environment during the mid-1950s. Specifically, after hatching, free embryos of *S. albus* drift downstream with the water currents and disperse several hundred km prior to transitioning from a dispersing free embryo to a benthic-oriented larvae (Kynard et al., 2007; Braaten et al., 2008, 2012). Although the specific recruitment stressor associated with Lake Sakakawea is not known, recent work on *S. albus* suggests that anoxic conditions in the river-reservoir transition zone serve as an agent of mortality for drifting free embryos (Guy et al., 2015).

Two lines of evidence lend support to the hypothesis that a mismatch (Kynard et al., 2007) between the length of free-flowing riverine habitat required by drifting free embryos and the length of riverine habitat available below hatch locations developed as Lake Sakakawea gradually filled. First, prior to closure of Garrison Dam in 1953, free embryos originating from spawning events in either or both the Missouri River and Yellowstone River were provided at least 309 km of free-flowing river extending from the confluence of the Missouri and Yellowstone rivers at rkm 2547 to the current location of Garrison Dam at rkm 2238. Additional free embryo drift distance was likely available depending on how far upstream spawning events occurred in either river system. Following closure of Garrison Dam, gradual filling of Lake Sakakawea decreased the length of free-flowing river available below the Missouri and Yellowstone rivers as water surface elevations in the reservoir increased from 529 m msl (1954) to 549 m msl (1957). If recruitment was curtailed after the mid-1950s, results suggest that the length of free-flowing river available to drifting *S. albus* free embryos may have been adequate during the first few years of reservoir filling; however, reservoir levels reached a critical point in the mid- to late-1950s that reduced the length of free-flowing river and diminished the likelihood of free embryo survival. Reservoir levels have fluctuated between 550 and 565 m msl since 1957; however, the extant stock of *S. albus* has experienced either recruitment failure or very limited recruitment for the years representative of these reservoir levels (USFWS, 2007, 2014).

A second line of evidence supporting the river-reservoir mismatch hypothesis for drifting free embryos originates from work initiated in 2007 focused on validation of spawning by *S. albus*. For the Yellowstone River, spawning has been verified multiple years since 2007 with spawning events occurring in the lower 12 km of the system (Fuller et al., 2008; Fuller and Braaten, 2012; DeLonay et al., 2014; Eichelberger et al., 2014). In addition, drifting free embryos from spawning events have also been collected from the Yellowstone River (Eichelberger et al., 2014) indicating that

environmental conditions are suitable for successful spawning, fertilization and hatch, and that drift-entry of free embryos occurs. Although speculative, these results suggest that conditions for *S. albus* spawning in the Yellowstone River have remained suitable since the closure of Garrison Dam and filling of the reservoir, and that spawning may occur annually. In contrast to the Yellowstone River where spawning may occur annually, altered flow and thermal regimes resulting from operations of Fort Peck Dam diminish suitability of the Missouri River for spawning *S. albus* (USFWS, 2000, 2014). A single account of successful spawning, hatch and drift entry of free embryos was documented in the Missouri River during 2011 when large flow events improved suitability for spawning (DeLonay et al., 2014). However, the extent to which spawning has occurred in the altered Missouri River following closure of Fort Peck Dam in 1937 is unknown. Collectively, spawning by *S. albus* does occur in the upper Missouri River basin, but recruits from spawning events during the late-1950s to present have not been detected.

Acknowledgements

This work was funded by the U. S. Army Corps of Engineers Missouri River Recovery Program – Integrated Science Program. The authors extend special thanks to B. Kuhajda (University of Alabama) for access to the whole-fish repository and preparing the frozen specimens for dissection. Thanks are also extended to R. Holm (U. S. Fish and Wildlife Service Garrison Dam National Fish Hatchery) for access to specimens, R. Wilson (U. S. Fish and Wildlife Service) for assistance obtaining mortality records for specimens, and D. Latka (U. S. Army Corps of Engineers) for providing Lake Sakakawea elevation data. A. MacDonnell and W. Joyce (Bedford Institute of Oceanography) provided the otolith micromilling and imaging expertise. M. Hamel and C. Paukert provided reviews on an earlier draft of the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U. S. Government.

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