

A Long-Term Program for Validation and Verification of Dentaries for Age Estimation in the Yellowstone–Sakakawea Paddlefish Stock

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Abstract.—An approach is described to assess the accuracy and precision of age estimates for paddlefish *Polyodon spathula* of the Yellowstone–Sakakawea stock in Montana and North Dakota. Twenty-five of 30 fish tagged with coded wire tags as age-0 fish in 1995 and recaptured over the period 2002–2005 were independently aged correctly with dentaries (lower jaw bones); estimates for the other five fish deviated from actual ages by 1 year. For fish older than age 10, estimated ages based on dentaries collected from 1991 to 2004 were compared with the estimated minimum expected ages of recovered fish that were jaw-tagged during 1964–2004. Of 323 fish, 300 (93%) had estimated ages that were the minimum expected age or older. The ages for the remaining 23 fish were less than the minimum expected ages, mostly by three or fewer years; these fish spanned a range of ages but tended to be older. Precision estimates (mean coefficient of variation) for age determination ranged from 3.6% for female fish from Montana in 2003 to 7.1% for male fish from North Dakota in 2003. The results indicate that estimating ages from Yellowstone–Sakakawea paddlefish dentaries is generally a repeatable, straightforward process with sufficient accuracy and precision to be useful for stock assessment. Validation studies should be conducted on other paddlefish stocks because the ease of interpreting dentaries varies with locality.

Effective fisheries management often depends on the ability to accurately and precisely determine the ages of fish (Bagenal 1973; Carlander 1987; Panfili et al. 2002). Reliable estimates of age are useful in assessing year-class strength, growth, mortality rates, and recruitment as part of harvest management and habitat management evaluations (DeVries and Frie 1996; Campana 2001).

Ideally, the structure and technique used for age determination (e.g., scales, otoliths, fin sections, vertebrae, or cleithra) should be both validated and verified to assess accuracy and precision (Casselman

1983; Heidinger and Clodfelter 1987; Campana 2001). Validation, which assesses accuracy, is commonly based upon counting the annual marks on the structure from fish previously tagged or marked at a known age. Verification, which assesses precision, typically refers to the degree of agreement among different persons in estimating the age. Although it has been argued that validation and verification should be performed in all situations, it is still not standard procedure in most age and growth studies (Beamish and McFarlane 1983; Campana 2001). As a rule, the longer lived the fish, the more difficult it is to obtain both accurate and precise estimates of age.

Age determination for the paddlefish, *Polyodon spathula*, an ancient zooplanktivorous chondrosteian fish of the Mississippi River and Missouri River drainages, was first reported by Adams (1931, 1942)

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using otoliths and dentaries (lower jaw bones). Counting annual rings on the mesial arm of dentary sections has become the preferred method of estimating ages. The method of age determination has been used in several localities (Russell 1986; Reed 1989; Reed et al. 1992), including Montana and North Dakota for the Yellowstone–Sakakawea stock (Scarnecchia et al. 1996).

Age validation of paddlefish dentaries has historically been hampered by the long life span of the species (estimated to exceed 50 years in some locations; Scarnecchia et al. 1996) as well as by the inability to tag adequate numbers of paddlefish of known age. In the late 20th century, several developments made it possible to assess the validity of estimated ages. These developments included the ability to rear young paddlefish (Michaletz et al. 1982; Mims et al. 1993) for possible release into the wild, the ability to sample (with dip nets) and subsequently release large numbers of wild age-0 fish (Scarnecchia et al. 1997), the ability to tag both hatchery-reared and wild age-0 fish with tags such as coded wire tags providing long-term retention (Guy et al. 1996; Scarnecchia et al. 1997), the implementation of long-term conventional tagging studies, as well as improved methods of cleaning, sectioning, and interpreting dentaries (Scarnecchia et al. 1996).

For the Yellowstone–Sakakawea paddlefish stock of eastern Montana and western North Dakota, age validation and verification are critical for harvest management of the recreational snag fisheries. Ages of harvested fish must be known to estimate the number of new recruits; the number of new recruits is then used to establish a harvest cap appropriate for a sustainable fishery. In the early 1990s it was recognized that in the absence of a revolutionary technology for age determination, a methodical, long-term plan for age validation would be important and should be implemented (Scarnecchia et al. 1995).

The objectives of this paper are to outline a method that has been implemented to validate paddlefish ages for the Yellowstone–Sakakawea stock and to present available evidence regarding validation and verification of paddlefish dentaries for estimation of ages. The approach and results outlined for the Yellowstone–Sakakawea stock have relevance to other paddlefish stocks throughout the species' range.

Study Site

The Yellowstone–Sakakawea paddlefish stock inhabits the lowermost 382 river kilometers (rkm) of the Yellowstone River (YR) from the Cartersville Diversion Dam, Montana, downriver to the confluence with the Missouri River (MR; hereafter called the

Confluence), and further downriver into Lake Sakakawea, a large (156,000-ha) Missouri River main-stem reservoir. This stock also inhabits the Missouri River above the Confluence for 302 rkm to the tailwaters of Fort Peck Dam, as well as the lower Milk River, which enters the Missouri River 16 rkm below Fort Peck Dam. Nearly all paddlefish of this stock rear in Lake Sakakawea. Recreational snag fisheries occur each spring on prespawning migratory fish ascending the rivers from Lake Sakakawea. Significant fisheries exist in the Missouri River in North Dakota at the Confluence (MR, rkm 2,544; YR, rkm 0) and the Pumphouse (MR, rkm 2,503), and on the Yellowstone River at the Fairview Bridge (YR, rkm 14.5). The main fishery in Montana occurs on the Yellowstone River immediately downstream of the Intake Diversion Dam (YR, rkm 114; hereafter called Intake).

Methods

Validation of Fish through Age 10

In a thorough review of age validation, Campana (2001) considered release of marked fish of known age as the most rigorous of the age validation methods. This method was implemented for the Yellowstone–Sakakawea paddlefish stock beginning in 1995 on the assumption that recovery of tagged fish in succeeding years and decades would allow future validation of progressively older fish.

Tagging.—As of 2005, age validation for younger fish (through age 10) involved tagging hatchery-reared and wild-caught age-0 paddlefish (from Lake Sakakawea) with batch coded wire tags (Nielsen 1992) and releasing the tagged fish into Lake Sakakawea. Age-0 hatchery-reared paddlefish of the Yellowstone–Sakakawea stock were stocked into Lake Sakakawea in 1995 (9,093 fish) and 1997 (9,994 fish). In August, prior to stocking, all fish were tagged with batch coded wire tags in the rostra using table-top tag injectors and head molds (Nielsen 1992). Distinct tag codes allowed tagged fish captured in recreational snag fisheries to be assigned to specific brood years. Beginning in 1996, wild age-0 paddlefish were captured with dip nets in the headwaters of Lake Sakakawea during July and August as part of annual monitoring and stock assessment activities (Fredericks and Scarnecchia 1997; Scarnecchia et al. 1997). Fish 150–275 mm in fork length (FL) in August, identified as age-0 fish by their size and from an observed annual pulse in numbers in late summer (Fredericks and Scarnecchia 1997), were held briefly in tanks on the boats, tagged with a hand-held tagger (without using a head mold), and released immediately. Over the period 1996–2004, 12,622 wild age-0 fish were captured, tagged, and released back into the reservoir.

Recovery of coded-wire-tagged fish.—Initial recoveries of harvested, coded-wire-tagged fish occurred in 2002 (1 fish), 2003 (2 fish), 2004 (4 fish), and 2005 (23 fish). Tags were detected with a hand-held detector in fish harvested by the recreational snag fisheries that had been brought to Intake and the Confluence for cleaning. Fish were measured and weighed, and dentaries were taken from each fish. Tags from the fish were removed by removing the distal end (tip) of the rostrum with a saw, and returning the tip to the laboratory for excision of the tag. The binary code on the tag was read and the tag assigned to a brood year. Dentaries were removed from the tagged fish with diagonal pliers and returned to the laboratory.

Validation of Fish Age 11 and Older

Tagging.—For fish age 11 and older, it was not possible as of 2005 to validate ages in the same manner as for fish less than age 11, because no tagged fish of known age could have returned that were older than age 10. However, we tested the plausibility of our estimated ages of older fish by comparing the estimated ages based on dentaries with the estimated minimum expected ages of the fish from recoveries of jaw-tagged fish. Over the period 1964–2004, adult migratory fish were captured for tagging with angling, gill nets, and seines, tagged with individually numbered metal (monel) or plastic poultry band tags around their dentaries, and released. Tagged fish were subsequently harvested in the fisheries, and in most cases since 1991, their dentaries were also retained and assessed for age. The fisheries harvest almost exclusively sexually mature, migratory fish which have been estimated to be nearly always age 8 or older for males, and age 15 or older for females (Scarnecchia et al. 1996). Validation of fish age 10 and younger in this study, if confirmed, would support the age estimates that lead to this conclusion. In this situation, fishes with increasingly longer periods between tagging and recapture would have been expected to have increasingly greater minimum ages. For example, if the minimum age of recruitment is age 8 for males and age 15 for females, tagged males recaptured at least 6 years after tagging would have been expected to be at least age 14 and tagged females at least age 21; tagged males recaptures 12 years after tagging would have been expected to be at least age 20 and tagged females at least age 27. In applying this approach, minimum age was plotted on the ordinate against number of years between tagging and recovery on the abscissa for all fish separately by sex. On such plots all individual fish, except for occasional precocious or immature upstream migrants, would have been expected to plot on or above the line depicting minimum expected age.

Significant numbers of fish below the line would indicate probable underestimation of age.

Recovery of jaw-tagged fish.—Tag recoveries were obtained from fish harvested at fishing sites along both the Missouri and Yellowstone rivers and brought for cleaning by anglers to the Confluence and Intake. Fish were measured, weighed, and identified as to gender. Dentary samples were taken.

Age Estimation

The protocol for cleaning, sectioning, and interpreting the dentaries is described in detail in Scarnecchia et al. (1996). Thin cross-sections of dentaries were interpreted for age with a Biosonics Optical Pattern Recognition System. Age estimation for validation followed a protocol established under the management plan for this stock (Scarnecchia et al. 1995). In the years 1991–1999, one experienced reader interpreted the sections and assigned an age. From 2000–2004, a two-reader, double-blind protocol was used, along with a tolerance for minor disagreement. In this protocol, each of two persons (designated primary and secondary readers) aged the sections separately. If there was agreement (plus or minus 1 year for fish under age 20, plus or minus 2 years for ages 20–34, and plus or minus three years for ages 35 and older), the final age was assigned by the primary reader. If the ages differed based on these criteria, the sections were read independently again. If the age estimates still did not meet agreement criteria, the section was aged with both readers in consultation and a final age was assigned by the primary reader. Ages of tagged paddlefish (coded-wire-tagged and jaw-tagged) were estimated along with a concurrent effort on other, untagged paddlefish sampled as part of annual fishery stock assessment. The tagged fish, identified only by their angler tag identification number, were not distinctly identifiable from the other fishes by those estimating the ages. Estimated ages of tagged fish were then compared with known ages of coded wire tagged fish (fish < age 11), or compared with estimated minimum ages of jaw-tagged fish (fish age 11 and older).

Verification

In addition to validation efforts for fish of known age, verification (precision) estimates were conducted in 2003 and 2004 using dentaries from harvested fish from both North Dakota and Montana. In 2003, ages were estimated for 834 fish (387 males, 447 females) caught in Montana and brought to Intake and for 790 fish (434 males, 356 females) caught in North Dakota and brought to the Confluence. In 2004, ages were estimated for 222 fish (100 males, 122 females) from

Intake and for 814 fish (412 males, 402 females) from the Confluence. For this analysis, the first independent age assessment for each reader for each fish was used. Precision, as determined by this two-reader, single-blind protocol was estimated by calculating the coefficient of variation (CV_j), expressed as

$$CV_j = \frac{100[\sum(x_{ij} - x_j)^2 / (R - 1)]^{1/2}}{x_j},$$

where x_{ij} is the i th age determination of the j th fish, x_j is the mean age estimate of the j th fish, and R is the number of times each fish is aged ($R = 2$). The CVs for each fish were summed and divided by the number of fish to estimate a mean CV over all fish (Campana 2001). Data were also plotted to investigate if CV tended to increase or decrease with increasing estimated age. In addition to these plots, mean CV values by males and females, by year (2003 and 2004) and by state (Montana and North Dakota) were compared with a nonparametric Wilcoxon–Mann–Whitney two-sample test to assess whether significant differences existed in precision of age estimation according to sex. A general linear model approach was also used to assess differences in CV according to year, sex, and state. In all tests, $P < 0.05$ was required for significance.

Results

Validation

Fish age 10 or younger.—Of the 30 coded-wire-tagged fish of known age recovered, the binary codes on the tags indicated that 1 fish was age 7, 2 were age 8, 4 were age 9, and 23 were age 10. All 30 fish were found to be hatchery-reared fish of the 1995 brood year. As of 2005, none of the wild coded-wire-tagged fish (which would have been a maximum of age 9) had yet been recaptured. Of the 30 fish of known age, 25 were estimated to be the correct age according to the two-reader, double-blind protocol. Age estimates for the other five fish differed from the known age by 1 year (Table 1; Figures 1–3).

Fish age 11 and older.—In all, 162 male fish and 161 female fish, which had been tagged and recaptured at least 5 years apart, also had matching dentaries available for age estimation. Of the 323 fish, 300 fish (93%) had estimated ages at least as great as the minimum expected age (Figures 4, 5). Twenty-three fish (7%; 11 males and 12 females) had estimated ages less than the minimum expected age. The 23 fish for which estimated ages were below minimum expected ages were in most cases aged as less than the minimum expected age by 3 years or less (Figure 5). The 23 fish were spread over a range of ages but occurred at a higher frequency for the oldest fish. Three of the nine male fish recaptured 10 or more years apart had

estimated ages less than the minimum expected age; three of the four females captured 17 or more years apart had estimated ages less than the minimum expected age. However, a female fish recaptured 24 years after tagging (tagged in 1978, recaptured in 2002) had a minimum expected age of 39 years and was estimated to be age 42.

Verification

Precision estimates for age determination, as indicated by mean CV for both sexes combined, were 4.0% ($N = 833$) for Montana fish and 6.2% ($N = 790$) for North Dakota fish in 2003. For 2004, mean CV was 5.1% ($N = 221$) for Montana fish and 4.9% for North Dakota fish ($N = 811$). No tendency was found for CV to increase with increasing age of the fish. In comparing CV values for male and female fish, significant differences ($P < 0.05$) were found for North Dakota in 2003 and for the combined North Dakota data from 2003 to 2004. No significant differences were found for Montana fish in 2003, 2004, or for both years combined, nor for North Dakota fish in 2004 (Wilcoxon–Mann–Whitney two-sample test: $P > 0.05$; Table 2). For Montana fish in 2003 and 2004 considered together, significant differences were found by year and sex, and by year (general linear model, $P < 0.05$). For North Dakota fish in 2003 and 2004, significant differences were found in CV by year and sex, by sex, and by the year \times sex interaction (general linear model: $P < 0.05$). For states and years combined, significant effects were detected by year, state, year \times sex interaction, and state \times year interaction (general linear model: $P < 0.05$; Table 2).

Using the two-reader, double-blind protocol with tolerance for minor disagreement (i.e., ± 1 year for fish under age 20, ± 2 years for ages 20–35, and ± 3 years for ages 35 and older), agreements after one reading in 2003 were 85% for Montana fish and 68% for North Dakota fish. Agreements in 2004 were 78% for Montana fish and 76% for North Dakota fish.

Discussion

Results of this study provide direct evidence that the rings or bands on dentaries described by Adams (1931, 1942) are annuli. He found the dentary to be the best structure for age determination and that the bands appeared to be annual or periodic (Adams 1931). Results of this paper establish the validity of dentaries for Yellowstone–Sakakawea paddlefish through age 10. The five deviations of estimated ages from actual ages were by only 1 year. Adams (1942) also observed that “there is little or no replacement of the bone and the original material is retained, so that the structures peculiar to the first year remain little changed even in

TABLE 1.—Length, weight, and age estimation (from a two-reader, double-blind protocol) and actual ages for 30 coded-wire-tagged age-0 male paddlefish (identified by angler tag number) released in White Earth Bay, Lake Sakakawea, North Dakota (ND), in 1995 and harvested in the Yellowstone River (YR) at rkm 114 and the Missouri River (MR) at rkm 2,544 during 2002–2004. Some lengths and weights were not available (NA).

Fish number	Date of capture	Length (mm)	Weight (kg)	Age (years)	
				Estimated	Actual
Yellowstone River					
MT0576	Jun 10, 2002	723	4.1	7	7
MT6567	May 22, 2003	762	6.8	9	8
MT2893	May 19, 2005	864	9.1	10	10
MT3629	May 20, 2005	864	9.1	10	10
MT3208	May 20, 2005	889	10.0	10	10
MT3191	May 20, 2005	838	7.3	10	10
MT2906	May 21, 2005	NA	6.8	10	10
MT2081	May 21, 2005	813	6.8	10	10
MT2818	May 21, 2005	914	9.1	10	10
MT5685	May 21, 2005	889	8.2	10	10
MT2093	May 21, 2005	838	8.6	10	10
MT4991	May 21, 2005	NA	NA	9	10
MT (NA)	May 21, 2005	864	7.7	10	10
MT3619	May 22, 2005	889	9.1	10	10
MT3571	May 22, 2005	838	8.2	10	10
MT10005	May 23, 2005	864	NA	10	10
MT1931	May 24, 2005	864	9.1	10	10
MT3442	May 24, 2005	864	8.6	10	10
MT0142	May 24, 2005	864	8.2	10	10
MT1774	May 24, 2005	864	9.5	10	10
Missouri River					
ND3403	May 17, 2003	813	7.3	8	8
ND0508	May 6, 2004	787	6.4	9	9
ND0064	May 7, 2004	737	5.0	10	9
ND4930	May 9, 2004	787	6.8	10	9
ND0607	May 16, 2004	787	5.9	8	9
ND2025	May 4, 2005	838	8.2	10	10
ND3078	May 6, 2005	813	9.5	10	10
ND0042	May 7, 2005	813	8.2	10	10
ND2703 ^a	May 8, 2005	838	8.6	10	10
ND1296	May 11, 2005	838	9.1	10	10

^a Yellowstone River at rkm 14.

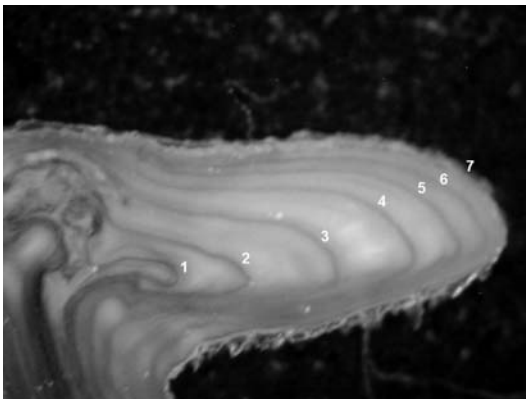


FIGURE 1.—Photograph of a dentary cross section from an age-7 paddlefish (MT0576) that was reared at Garrison National Fish Hatchery, North Dakota; tagged with a coded wire tag at age 0; released in White Earth Bay, Lake Sakakawea, North Dakota; and recaptured at the Intake Diversion Dam on the Yellowstone River, Montana, on June 10, 2002. The seventh annulus (annuli are numbered) is on the edge, indicating a fish caught in spring or early summer.

old specimens” (Adams 1942:629). His observation of no loss of bone differs from the loss described for fin rays in white sturgeon *Acipenser transmontanus* (Veinott and Evans 1999). Adams’ (1942) observations on paddlefish dentaries are corroborated by our results, in which the first annulus is clearly visible (Figures 1–3).

Validation of dentaries for young paddlefish recruits is consistent with indirect evidence of validity from other sources. Adams (1942; his Plate 2) correlated the size of fish with the number of putative annuli. Other investigators have reported similar positive relations between fish size and number of putative annuli (Rosen et al. 1982; Russell 1986). For the Yellowstone–Sakakawea stock (Scarnecchia et al. 1996; Scarnecchia, unpublished), distinct, pronounced annual differences in estimated age-at-maturity between harvested males and females (which consisted almost exclusively of sexually mature fish) provided strong indirect evidence that ages of new recruits (less than age 20) were accurate. Among Montana-harvested paddlefish

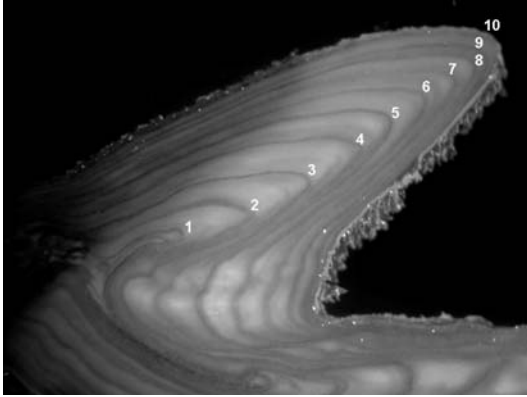


FIGURE 2.—Photograph of a dentary cross section from an age-10 paddlefish (MT3619) that was reared at Garrison National Fish Hatchery, North Dakota; tagged with a coded wire tag at age 0; released in White Earth Bay, Lake Sakakawea, North Dakota; and recaptured at the Intake Diversion Dam on the Yellowstone River, Montana, on May 22, 2005. A distinct false annulus (halo band; annuli are numbered) is visible between annuli 6 and 7.

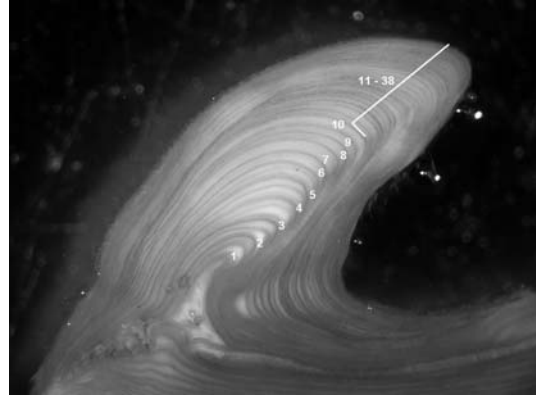


FIGURE 4.—Photograph of a dentary cross section from a female paddlefish (ND0024) tagged with a plastic jaw tag on September 27, 1994, at rkm 2,533 on the Missouri River and recaptured 10 years later (May 13, 2004) in the lower Yellowstone River (rkm 25). The minimum expected age was 25; the estimated age from dentary examination was 38 (annuli are numbered).

brought to Intake in 2003, 257 of 387 male fish (66%) were estimated to be less than age 15, whereas none of 447 female fish (0%) were estimated to be less than age 15. Among North Dakota harvested fish brought to the Confluence, 84 of 434 male fish (19%) were estimated to be less than age 15, whereas only one of 356 female fish (0.3%) was estimated to be less than age 15. These distinct differences in assigned ages between males and females occurred even though the gender of the fish

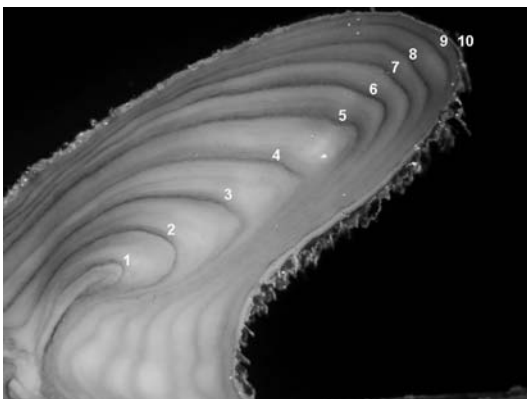


FIGURE 3.—Photograph of a dentary cross section from an age-10 paddlefish (MT3351) that was reared at Garrison National Fish Hatchery, North Dakota; tagged with a coded wire tag at age 0; released in White Earth Bay, Lake Sakakawea, North Dakota; and recaptured at the Intake Diversion Dam on the Yellowstone River, Montana, on May 21, 2005. The annuli are numbered.

was unknown to the readers at the time of age estimation. Even with this strongly suggestive indirect evidence, however, actual validation of annuli is considered necessary for the proper application of the method (Beamish and McFarlane 1983; Campana 2001).

Five of the 30 known-age fish were estimated at ± 1 year rather than the exact age. The most common problems associated with identifying annuli on these 30 dentaries and many others we have analyzed involve the first annulus, the last annulus, and false annuli, or halo bands, that may be present, especially between pairs of the first 10 annuli (Figures 2, 4). The first annulus may be misinterpreted because of differences in cross-sectional cuts among fish (Adams 1942), from differential growth among fish, or other factors. The last annulus may or may not yet be fully formed or formed at all on the edge of the section for a fish caught in spring. The cause of halo bands is not specifically known. We suggest that they may be a result of growth retardation or cessation during the warmest summer periods or other abrupt habitat changes. The importance of this minor inaccuracy to management decisions will depend on how prevalent it is (i.e., most fish or just a few fish) and the accuracy needed for a particular application. In addition, we have observed first-hand that dentaries from some other paddlefish stocks (e.g., Kentucky, Tennessee, and Oklahoma) may have more halo bands than our fish and are often more difficult to interpret for ages. For that reason, we recommend that age validation be pursued indepen-

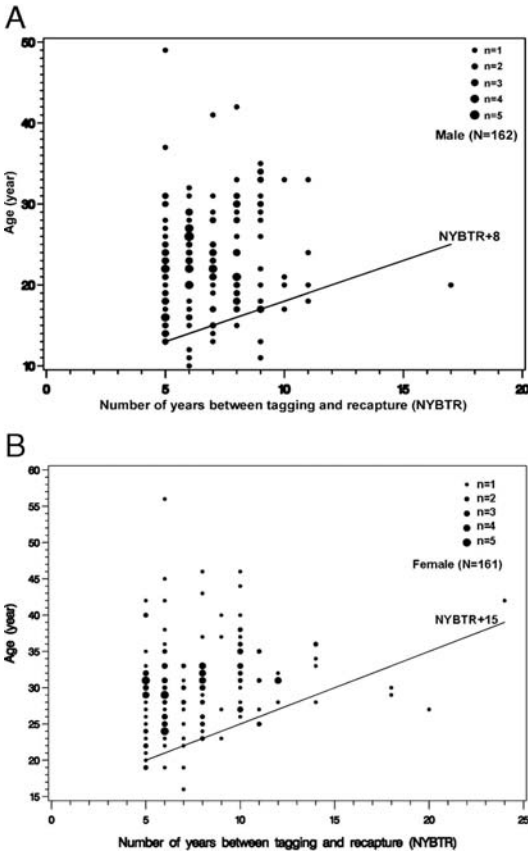


FIGURE 5.—Comparison of age estimates for male (top panel) and female (bottom panel) paddlefish from the Yellowstone and Missouri rivers recaptured at least 5 years after tagging and the minimum expected ages of the fish. The diagonal line (NYBTR + 8 for males; NYBTR + 15 for females) is the locus of points indicating the number of years between tagging and recapture (plus 8 years for males and 15 years for females), which is the estimated minimum age at first recruitment and the youngest age at which upstream-migrating fish were assumed to be available for tagging.

dently for other paddlefish stocks as part of other stock monitoring programs.

Although an insufficient number of years has elapsed for true validation of ages for fish older than age 10, results of this study indicated that in 93% of the cases, ages determined from dentaries were consistent with minimum expected ages of fish. The tendency for estimated fish age to be less than the expected minimum increased with the age of the fish but did not appear to be substantial or to necessarily apply to all fish. In most cases older fish of a particular minimum expected age showed as many or more than the expected number of annuli (Figures 4, 5). Underestimation of the age of older fishes of various

TABLE 2.—Mean estimates of coefficients of variation (CVs; Wilcoxon–Mann–Whitney two-sample test, one-sided) and significant effects (general linear model on rank CV) for age estimates for male and female paddlefish captured in 2003 and 2004 from Montana and North Dakota. Significant values ($P < 0.05$; one-tailed test) are given in bold italics; two-tailed test results, which are double the presented P -values, do not differ in significance.

State, year, and variable	Sex		P -value	Significant effects
	Male	Female		
Montana				
2003	4.51 (5.35)	3.55 (3.39)	0.167	
2004	4.84 (8.51)	5.38 (8.64)	0.061	
Combined	4.58 (6.13)	3.94 (5.04)	0.470	Year
North Dakota				
2003	7.06 (6.74)	5.21 (5.02)	<0.0001	
2004	5.45 (7.45)	4.35 (4.44)	0.480	
Combined	6.28 (7.13)	4.76 (4.74)	0.0006	Sex Year × sex
Montana ^a				
Year and sex			<0.0001	
Year			<0.0001	
Sex			0.933	
Year × sex			0.368	
North Dakota ^a				
Year and sex			0.0006	
Year			0.228	
Sex			0.003	
Year × sex			0.004	
Both states ^a				
Sex			0.0017	
Sex and state			<0.0001	
State			<0.0001	
Sex			0.0178	
State × sex			0.0224	
Sex, year, and state			<0.0001	
Sex			0.0820	
Year			<0.0001	
State			<0.0001	
Year × sex			0.0190	
State × sex			0.1085	
State × year			<0.0001	
State × year × sex			0.3593	

^a 2003 and 2004 combined.

species has been reported widely. In some instances, such as for the sablefish *Anoplopoma fimbria*, the underestimation has been discovered from designed marking or tagging studies (e.g., McFarlane and Beamish 1995). In most cases, however, underestimation has been discovered as better age determination capabilities have developed, either through the use of different calcified structures (e.g., otoliths, as opposed to scales, for arctic char *Salvelinus alpinus*; Nordeng 1961), as newer technologies have improved the ability to discern closely packed annuli (Casselman 1983), as entirely new techniques have developed (e.g., radiometric aging; Smith et al. 1995), or a combination of factors (Prince et al. 1995). Although some underestimation of ages apparently occurs for the Yellowstone–Sakakawea stock, the problem is not considered

to be of large magnitude or a critical concern for harvest management.

Because of concerns about underestimation of ages of long-lived species, numerous investigators have attempted to shorten the process of validation by marking of fish of unknown age with oxytetracycline and recapturing them a known number of years later (e.g., for white sturgeon; Rien and Beamesderfer 1994; Rossiter et al. 1995). Putative annuli produced in the intervening years are counted and evaluated for accuracy. This approach only validates individual annual marks between marking and recovery, however, and may not provide an accurate estimate of the fish's age. In the absence of true validation of fish of known age, managers should develop appropriate harvest models that will produce reliable estimates of sustainable yields even if ages of old fish are not perfectly validated, or are slightly underestimated.

The precision estimates for Yellowstone–Sakakawea paddlefish reported in this study (range, 3.55–7.06) are below the median CV of 7.6% reported by Campana (2001) from a summary of 117 published values over a variety of calcified structures, including scales, otoliths, fin rays, and spines. They are also lower than for Columbia River white sturgeon fin rays (7.8%; Rien and Beamesderfer 1994). The results support our observations, based on more than 23,000 paddlefish age estimates over a 15-year period (1991–2005), that estimating ages from Yellowstone–Sakakawea paddlefish dentaries is in most cases a repeatable, straightforward process. Despite the favorable degree of precision overall, however, the amount of imprecision varied with year, sex, and state in an inconsistent manner (Table 2). In our study, the same primary reader interpreted sections in both 2003 and 2004, but two different second readers were employed in the 2 years. The inconsistent differences in CV by year, sex, and state may thus reflect slightly different interpretations of particular readers rather than actual differences in precision associated with a particular year, sex, or state.

Our validation and verification program has been designed not just for one-time assessment but as part of long-term tagging, recovery, and monitoring efforts. In future years, we anticipate recoveries of more hatchery-reared fish as well as wild fish and thus better evaluation of the accuracy and precision of estimated ages for progressively older fish.

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