

Accuracy and Precision of White Sturgeon Age Estimates from Pectoral Fin Rays

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Abstract.—Multiple readings and recaptures of marked fish were used to estimate precision and accuracy of age estimates from cross sections of pectoral fin rays of white sturgeons *Acipenser transmontanus* collected in impoundments of the Columbia River. Ages ranged from 2 to 104 years but only 37% of samples were assigned the same age by two readers. Percent error in multiple readings averaged 5.9% and the coefficient of variation averaged 7.8%, indicating low precision relative to reported values for other species. An injected dosage of 25 mg oxytetracycline (OTC) per kilogram of body weight marked 216 of 220 fin ray samples for validation and did not reduce white sturgeon growth. Accuracy was improved by identifying the period of annulus formation (May–June) from the position of an OTC mark relative to translucent zones in fin ray cross sections. However, age was underestimated from counts of translucent zones formed after injection with OTC, especially for slow-growing and large fish. We conclude that age estimates were not precise or accurate and recommend development of alternative methods for aging white sturgeons to supplement the fin ray method. We urge that aging data based on the fin ray method be applied cautiously. Imprecision limits interpretation of age frequencies and relative year-class strengths. Inaccuracy results in overestimation of growth, mortality, and sustainable exploitation rates.

Estimates of growth and mortality biased by inaccurate aging of fish can lead to gross errors in management of long-lived stocks (Beamish and Chilton 1982; Archibald et al. 1983; Beamish and McFarlane 1983; Leaman and Nagtegaal 1987). Validation is therefore a crucial component of age and growth studies (Brothers 1982; Beamish and McFarlane 1983; Jearld 1983). Even when valid methods are used, difficulties in interpretation contribute uncertainty to age estimates (Richards et al. 1992). This uncertainty may affect confidence in applications of age data for management decisions (Lai and Gunderson 1987) and for analysis of year-class strength (Bradford 1991).

Oxytetracycline (OTC) has been used to validate ages assigned from counts of periodic marks on bony structures of fish (Beamish and McFarlane 1983; Babaluk and Campbell 1987; Leaman and Nagtegaal 1987; Tzeng and Yu 1989), but its use has not been evaluated for sturgeons *Acipenser* spp. McFarlane and Beamish (1987) found that mortality of sablefish *Anoplopoma fimbria* increased in direct proportion to dosage rate of OTC; however, OTC marking effectiveness was substantially reduced at low dosages. They recommended using dosages that maximize the number of marked fish recaptured. Monaghan (1993) observed that OTC dosages of 25–50 mg/kg of body weight were detrimental to fish health.

Sturgeon ages are commonly estimated from

cross sections of pectoral fin rays (Cuerrier 1951; Probst and Cooper 1955; Dadswell 1979; Kohlhorst et al. 1980; Jearld 1983; Smith et al. 1984; Threader and Brousseau 1986; Wilson 1987; Guénette et al. 1992; Keenlyne and Jenkins 1993). Brennan and Cailliet (1989) evaluated a variety of calcified age structures (pectoral fin rays, opercles, clavicles, cleithra, medial nuchals, and dorsal scutes) used to age white sturgeons *Acipenser transmontanus* and found that ages estimated from these structures did not vary significantly. They concluded that pectoral fin rays provided the greatest reader precision, and unlike other structures (opercles, clavicles, cleithra, and medial nuchals), fin rays can be collected without killing fish. However, the validity of this method has not been fully established. Brennan and Cailliet (1991) examined OTC-marked fin rays from 19 white sturgeons at large for more than 1 year after marking and found one translucent and one opaque zone were generally formed for each year at large. An exception was one fish that made a long ocean migration and showed little growth after the OTC mark in the fin ray. Other studies have suggested that two translucent zones may form annually in some sturgeons (Sokolov and Malyutin 1978).

In this paper we report on the precision and accuracy of aging white sturgeon from impoundments of the Columbia River by using pectoral fin rays.

TABLE 1.—Fork lengths and ages of white sturgeons injected with oxytetracycline and recaptured in three reservoirs of the Columbia River. *N* is the number of fish injected in each year.

Fork length (cm)	Age (years) ^a	Injected 1988				Injected 1989				Injected 1990			Injected 1991		
		<i>N</i>	Number recaptured in:				<i>N</i>	Number recaptured in:			<i>N</i>	Number recaptured in:		<i>N</i>	Number recaptured in 1991
1–20	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
21–40	1–10	2	0	0	0	0	1	0	0	0	51	3	0	109	1
41–60	2–17	104	0	1	0	2	450	1	1	6	154	8	3	527	3
61–80	1–24	509	0	24	0	11	1,687	6	0	38	335	11	9	1,065	15
81–100	6–30	140	0	11	0	16	418	5	0	25	76	6	1	316	5
101–120	8–34	0	0	0	0	1	0	0	2	3	0	0	0	4	0
161–180	14–34	2	0	0	0	1	3	0	0	0	3	0	0	8	0
181–200	18–40	1	0	0	0	0	8	0	0	0	13	1	0	9	0
201–220	17–51	0	0	0	0	0	13	0	0	0	9	0	0	10	0
221–240	22–60	0	0	0	0	0	8	0	0	0	5	0	0	8	0
241–260	29–80	0	0	0	0	0	2	0	0	0	0	0	0	3	0
261–280	37–104	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Total		758	0	36	0	31	2,590	12	3	72	646	29	13	2,062	24

^a T. A. Rien and colleagues (Oregon Department of Fish and Wildlife, unpublished data, 1991).

Methods

Ages of white sturgeons were estimated by counting annuli on cross sections of anterior pectoral fin rays. All fish were from three Columbia River impoundments—Bonneville (74 km long, 8,400 hectares), McNary (38 km, 4,500 hectares), and John Day (123 km, 21,000 hectares).

White sturgeons were captured with set lines and by anglers (Elliott and Beamesderfer 1990; Hale and James 1992). We injected 6,056 white sturgeons with OTC in April–August, 1988–1991. Although the fork length range of injected fish was broad (19–280 cm), most fish were 41–100 cm (Table 1). An OTC concentration of 100 mg/mL was injected into red muscle tissue under the dorsal scutes just behind the head. A dosage of 25 mg OTC/kg of body weight was used (Leaman and Nagtegaal 1987; McFarlane and Beamish 1987). Only white sturgeons shorter than 85 cm or longer than 170 cm were injected so that anglers, who can legally keep fish 92–165 cm long, would not risk eating flesh from an injected fish during the 15-d withdrawal period suggested by the U.S. Food and Drug Administration. We marked all injected fish by removing the second right lateral scute, and we tagged all fish longer than 64 cm with uniquely numbered spaghetti tags.

We removed a section of the leading pectoral fin ray from live fish by making two cuts with a hacksaw blade or coping saw through the leading ray; the first cut was about 5 mm distal from the point of articulation and the second was about 10 mm distal from the first. We took care not to sever

the artery running close to the fin ray articulation. The fin ray section was then removed by twisting it free with a pair of pliers and inserting a knife between the first and second fin ray as needed. From dead fish, we removed the entire first fin ray. Among recaptured white sturgeons, we removed fin ray samples only from fish previously injected with OTC. We air-dried the fin ray samples and cut them into several thin (0.3–0.6-mm) transverse sections using a Buehler Isomet low-speed saw. The sections were mounted on glass microscope slides with clear fingernail polish.

Fin ray sections were examined with a dissecting microscope (15–40× magnification) and transmitted light. We considered translucent zones in the sample to be annuli (Brennan and Cailliet 1989). We observed that single translucent zones in the anterior portion of a sample often split into several zones in the lobes, a pattern we refer to as banding; banding occurred in fish of all ages. Each translucent zone of a banding pattern was counted as an annulus. Because it was difficult to determine if the edge was translucent or opaque (a problem also noted by Brennan and Cailliet 1989), translucent zones on the outer edge of a sample were not counted. Instead, we assumed all fish sampled before July 1 would form a translucent zone in that calendar year and grouped them with the appropriate cohort. We determined annulus formation was complete by July 1 using methods described later in this paper.

Precision of aging was estimated by comparing ages assigned to 935 fin ray samples aged twice by

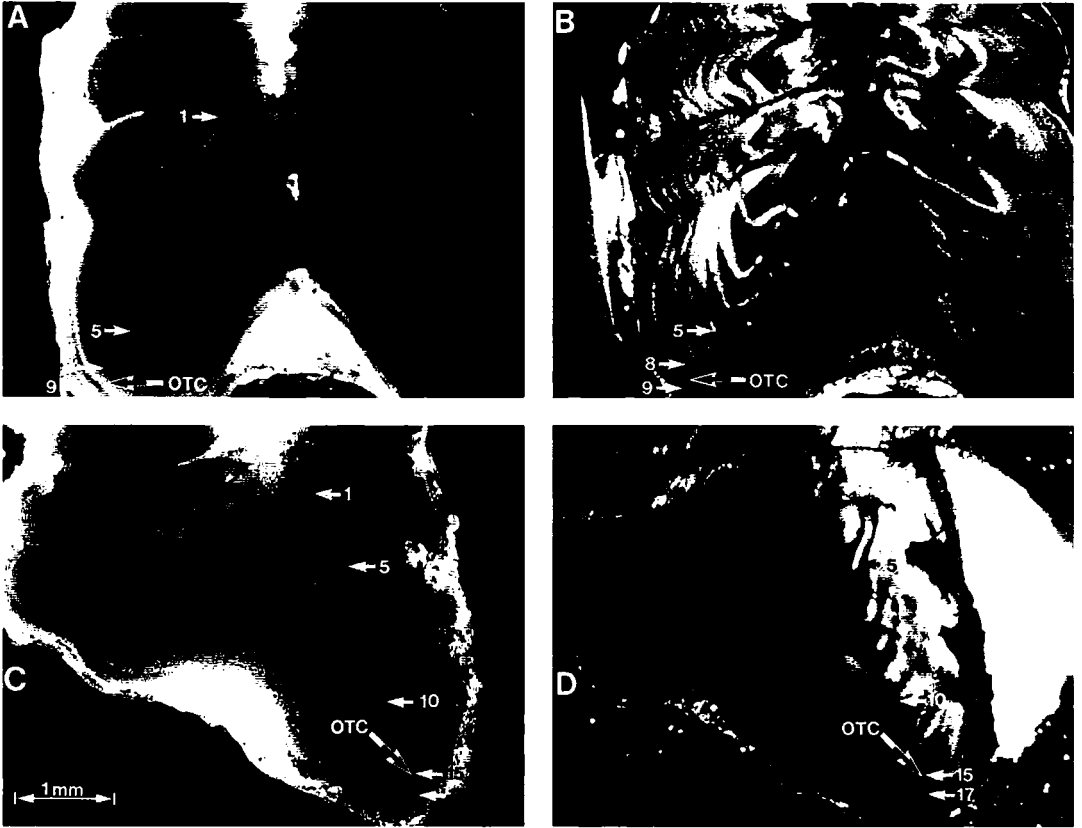


FIGURE 1.—Relative positions of annuli (numbered) and oxytetracycline (OTC) marks in white sturgeon fin ray sections resulting from injection of OTC outside the period of annulus formation (A, B) and during the period of annulus formation (C, D). Photographs A and C were exposed under ultraviolet light and show the position of fluorescing OTC marks. Photographs B and D were exposed under white light and show the relative positions of annuli. The sample in photographs A and B is from a fish injected with OTC on 28 August 1990 (71 cm fork length) and recaptured on 25 June 1991 (70 cm). The sample in photographs C and D is from a fish injected with OTC on 10 May 1989 (76 cm) and recaptured on 8 May 1991 (79 cm).

two readers. The readers (not the authors) had 2 and 3 years of experience aging white sturgeons from fin rays. Precision was described by means of percent agreement between readers, average percent error (APE), coefficient of variation (CV = 100 · SD/mean), and an index of precision (D). Percent agreement was the percentage of age assignments that fell within a specified number of years. We calculated APE and CV to allow comparisons of aging precision among species with widely differing life spans (Beamish and Fournier 1981; Chang 1982). Beamish and Fournier (1981) presented APE as

$$APE = \frac{1}{N} \sum_{j=1}^N \left[\frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - X_j|}{X_i} \right] \times 100,$$

where N is the number of fish aged, X_{ij} is the i th

reading of the j th fish, X_j is the average inferred age of the j th fish, and R is the number of readings of a sample. We present CV as the mean value calculated for all samples. Lower values for APE and CV represent greater precision. To provide an estimate of the percent error contributed by each observation we calculated D as $CV/R^{0.5}$ and present the mean value for all samples (Chang 1982).

Accuracy of aging was estimated with reference to OTC marks in sections from fish recaptured at known intervals after injection. The OTC marks on fin ray samples were located with reflected ultraviolet light. We determined the proportion of samples that were marked to describe marking effectiveness of the OTC dosage. We calculated annual growth increment as

$$(365.25 \text{ d/year})(L_R - L_C)/(\text{days at large}),$$

TABLE 2.—Frequency of differences in final fin ray ages assigned by two readers for white sturgeons collected in three reservoirs of the Columbia River, 1987–1991.

Age difference ^a	Final assigned age (years)													Total	Percent ^b		
	2	3	4	5	6	7	8	9	10	11–15	16–20	21–25	26–30			31–104	
-10															1	1	0.1
-9															1	1	0.1
-8													1		1	2	0.2
-7															2	2	0.2
-6										2	1	1			2	6	0.6
-5										1	2	2	1		2	8	0.9
-4										2	3	6	3		3	18	1.9
-3		1			5	1			1	4	16	6	5	3	44	4.7	
-2		1		5	2	5	4	4	5	16	20	11	9		82	8.7	
-1	1	4	2	3	13	15	13	10	14	30	25	24	7	6	167	17.9	
0	2	8	24	26	26	24	16	28	19	62	81	25	7	2	350	37.4	
1		1		1	3	4	8	5	5	29	40	21	3	1	121	12.9	
2				1				2	1	14	18	12	10	1	59	6.3	
3									2	7	10	12	4	2	37	4.0	
4				1					1	2	3	2	1	2	12	1.3	
5										2	2	4	2		10	1.1	
6										1	3	3			7	0.8	
7												3			3	0.3	
8											1	1		1	3	0.3	
9											1				1	0.1	
10													1		1	0.1	
Total	3	15	26	37	49	49	41	53	47	172	226	134	53	30	935	100.0	

^a Reader 1 minus reader 2.

^b Percent of 935 comparisons.

where L_R is length at recapture and L_C is length at first capture (Manire and Gruber 1991). Analysis of variance (ANOVA; SAS Institute 1988a) was used to compare annual growth increment among groups of recaptured fish that had and had not been injected. Fish that had not been injected (the control group) were first captured in 1987 and 1988, but were otherwise similar in size and handling to the group that was given OTC (the treatment group). We assumed differences in annual growth increment would indicate effects of OTC injection.

We compared proximity of OTC marks and the translucent zone to month of injection to determine the month of annulus formation. We assumed that OTC marks separate from the trans-

lucent zone indicated injection after annulus formation was complete (Figure 1A, B), and that an OTC mark in or abutting the translucent zone indicated injection during the period of annulus formation (Figure 1C, D). Statistical comparisons of OTC mark position among injection months were made with Fisher's exact test of independence (Sokal and Rohlf 1981; SAS Institute 1988b).

To validate our aging technique, six readers with at least 1 year of experience aging white sturgeons independently assigned an age to samples from OTC-injected fish using the OTC mark as zero. We will refer to this assignment as the OTC age, which corresponds to the number of years fish were at large between marking and recapture. Readers counted all translucent zones formed en-

TABLE 3.—Comparison of mean annual growth increment (fork length, cm) for tagged white sturgeons recaptured after 0–3 years at large among groups of fish injected and not injected with oxytetracycline (OTC). Fish were injected with OTC from 1988 through 1991; fish not injected were initially captured primarily in 1987 and 1988. All fish were 65–84 cm at marking.

Years at large	Injected			Not injected			Total		
	Increment (cm)			Increment (cm)			Increment (cm)		
	Mean	SE	N	Mean	SE	N	Mean	SE	N
0	3.89	1.39	95	1.88	1.83	21	3.53	1.18	116
1	1.87	0.47	37	0.11	0.63	23	1.20	0.39	60
2	2.30	0.49	46	1.58	1.27	4	2.24	0.46	50
3	2.63	0.64	21	1.20		1	2.57	0.61	22
Total	3.02	0.68	199	1.01	0.84	49	2.62	0.57	248

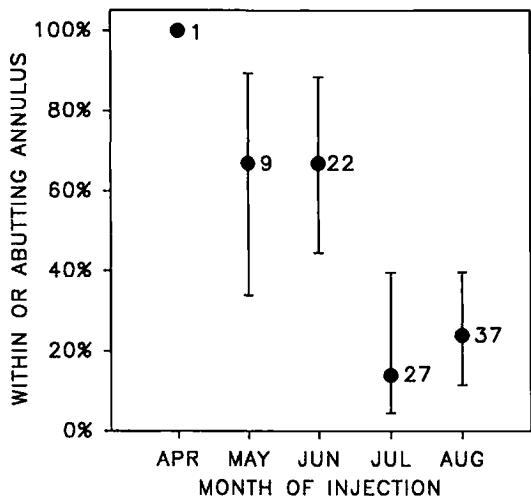


FIGURE 2.—Percentages of pectoral fin ray samples showing an oxytetracycline (OTC) mark in or abutting a translucent zone for white sturgeons previously injected with OTC in the Columbia River, 1988–1989. The number of samples and 95% confidence interval are shown with each data point.

tirely after the OTC mark. Translucent zones abutted by or containing an OTC mark were not counted.

We compared the OTC age assignment to the number of years at large for each sample examined. Accuracy was calculated as the percentage of all OTC age assignments that matched the number of years at large; it was compared among samples grouped by number of years at large and by length. For each sample, we calculated an average error in OTC age assignment as the difference between the number of years at large and the OTC age assigned. This was compared with the annual growth increment. We also examined variability in growth among all tagged fish that were recaptured, including those not injected with OTC.

Results

Ages assigned to 935 fin ray samples in four readings by two readers ranged from 2 to 104 years, but only 37% of the samples were assigned the same age by both readers; 68% of comparisons were within 1 year, 83% were within 2 years, and

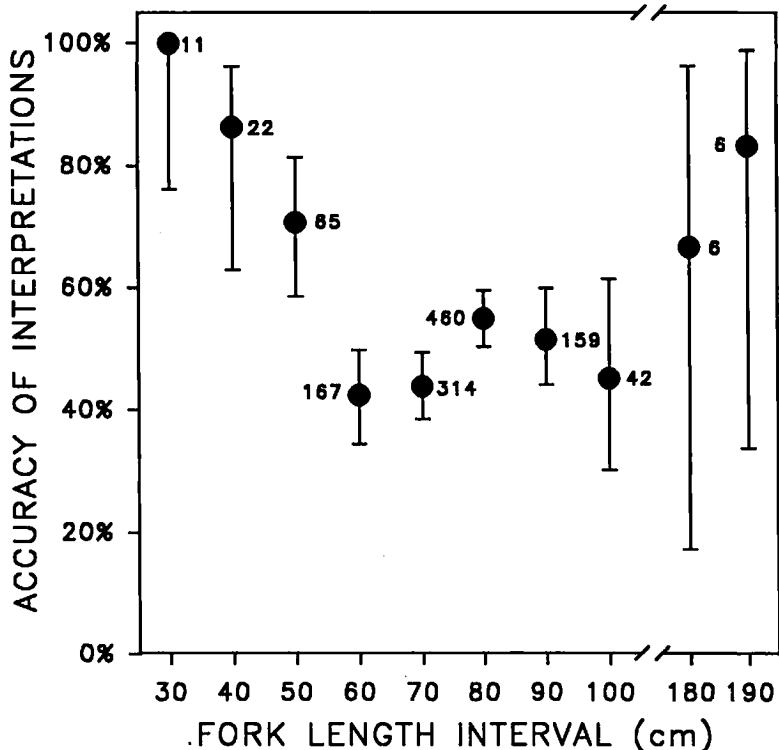


FIGURE 3.—Accuracy of period at large interpreted by six experienced readers examining white sturgeon pectoral fin ray sections collected from fish injected with oxytetracycline and recaptured after a period of up to 3 years in Columbia River impoundments, 1988–1991. We defined accuracy as the percentage of interpretations that matched the actual number of years at large. The number of readings and 95% confidence interval are shown with each data point.

TABLE 4.—Distribution of translucent zone counts outside the oxytetracycline (OTC) mark on pectoral fin ray sections of white sturgeons injected with OTC 0–3 years previously. Samples were independently examined by six trained readers with 1–6 years experience aging white sturgeons.

Years fish were at large	Number of samples	Number of readings	Translucent zone count					Accuracy ^a
			0	1	2	3	4	
0	65	376	342	33	1	0	0	91%
1	47	278	110	129	35	4	0	46%
2	73	433	167	105	119	40	2	28%
3	31	184	23	36	54	61	10	33%
Total	216	1,271						51%

^a The percentage of readings that agreed with known years at large.

91% were within 3 years (Table 2). Measurements of precision among all readings were APE = 5.89, CV = 7.80%, and D = 3.91.

We detected an OTC mark in 216 of 220 fin rays (98%) from white sturgeons that had been injected with OTC up to 3 years earlier. Mean annual growth increment was larger among white sturgeons injected with OTC than among fish that had not been injected (Table 3), but differences were not significant. Two-way ANOVA (type III

sum of squares) showed that annual growth increment did not vary significantly between OTC-injected and noninjected fish ($df = 3, 244; F = 0.12; P = 0.73$) and that the interaction between injection status and years at large also was not significant ($df = 3, 244; F = 0.00; P = 0.98$).

We recaptured 96 white sturgeons for which we could determine the month and year of OTC injection from records. Fin ray samples from white sturgeons injected before July 1 had a higher pro-

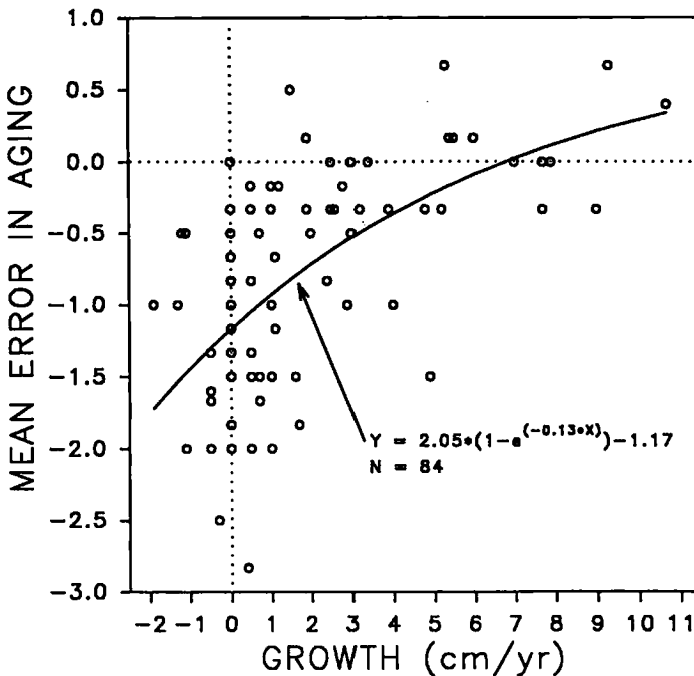


FIGURE 4.—Mean error (Y) in years at large interpreted from white sturgeon pectoral fin ray samples versus annual white sturgeon growth (X , fork length) in Columbia River impoundments, 1989–1991. White sturgeons had been at large at least 1 year after injection with oxytetracycline (OTC). Each data point represents the average difference between true periods at large and the OTC ages assigned for samples independently examined by six experienced readers.

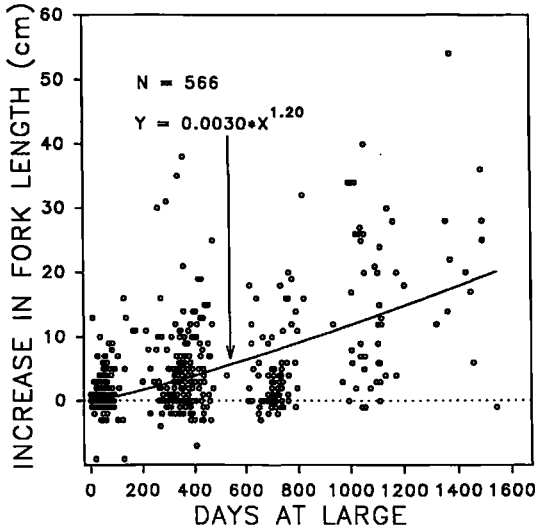


FIGURE 5.—Increase in fork length of tagged white sturgeons at large for up to 4 years prior to recapture in Columbia River impoundments, 1987–1991. Fish may or may not have been injected with oxytetracycline prior to recapture. Extreme values may represent errors in measurement or data recording.

portion of OTC marks in or abutting a translucent zone than did those injected on or after July 1 (Figure 2). The proportion of fin ray samples that showed an OTC mark in or abutting a translucent zone varied significantly among injection months (Fisher’s exact test: $df = 4$; $P < 0.001$).

Accuracy of OTC age interpretations declined

dramatically as period at large increased (Table 4). Many samples at large 1 or more years were underaged.

Accuracy of OTC age interpretation decreased as fork length increased (Figure 3). More than 70% of white sturgeons less than 60 cm were assigned the correct OTC age. Among larger fish (up to 100 cm) accuracy was less than 60%. Only two fish larger than the legal slot limit were recaptured.

Slow-growing white sturgeons were more likely to be underaged than faster-growing fish (Figure 4). The magnitude and bias of mean error in OTC age assignment were less among faster-growing fish. However, most recaptured white sturgeons had grown slowly; 59% of tagged fish at large 1 or more years grew less than 4 cm/year (Figure 5).

Discussion

Precision of age estimates from white sturgeon pectoral fin rays is low compared with precision measures reported for other species (Table 5). Both APE and CV are unbiased estimators of precision that allow comparison among species with widely different maximum ages (Chang 1982). Among literature values reported for 10 species, only star-spotted smoothhound and sablefish analyses had higher values of APE or CV for between-reader comparisons. Notably, these are long-lived species also, and the lower precision probably reflects a general tendency for annuli to be difficult to interpret in old fish due to reduced growth rates. The difficulties we experienced were primarily crowded translucent zones and variable-width

TABLE 5.—Percent agreement, average percent error (APE), coefficient of variation (CV), and indices of precision (D) for between-reader aging precision reported for various species.

Species	Study ^a	Percent agreement			APE	CV	D	Maximum age observed
		Complete	Within 1 year	Within 2 years				
White sturgeon	1	37	68	83	5.9	7.8	3.9	104
	2	17–31	57–63	77–84				
	3	23	55	74				
	4	32	74	95				
Blue shark <i>Prionace glauca</i>	5	5–53	6–100	58–100			7.4–21.8	90
Starspotted smoothhound <i>Mustelus manazo</i>	6	10–50	70–83	83–97	6.9–12.7		6.9–12.7	20
Pacific hake <i>Merluccius productus</i>	7	79				3.2		16
Yellowfin sole <i>Pleuronectes asper</i>	7	61				3.2		26
Pacific ocean perch <i>Sebastes alutus</i>	7	41				4.9		78
Walleye pollock <i>Theragra chalcogramma</i>	7	64				5.0		13
Atka mackerel <i>Pleurogrammus monopterygius</i>	7	67				6.8		10
Sablefish	7	43				12.9		29
Northern pike <i>Esox lucius</i>	8	88	93	98	1.2	1.2	0.8	11

^a Study: (1) this study; (2) Brennan and Cailliet (1989); (3) Shirley (1987); (4) Kohlhorst et al. (1980); (5) Tanaka et al. (1990), G. M. Cailliet (personal communication); (6) Cailliet et al. (1990), G. M. Cailliet (personal communication); (7) Kimura and Lyons (1991); (8) Laine et al. (1991).

opaque zones, as reported by Brennan and Cailliet (1989). We also saw and counted faint translucent zones, but did not see the "marbled" opaque zones reported for hatchery-reared white sturgeons (Brennan and Cailliet 1991). Our measures of percent agreement are similar to those reported for white sturgeon in California. This lack of precision will limit the utility of age assignments for analysis of population dynamics. For example, relative year-class strength would be difficult to detect from age frequencies except from those of very young fish.

Oxytetracycline injected at a dosage of 25 mg/kg of body weight effectively marked white sturgeons at a rate (98%) greater than McFarlane and Beamish (1987) reported for sablefish (70%) that had been given a similar dosage. McFarlane and Beamish (1987) also noted increased mortality at high dosages. Our sampling design did not allow us to measure differences in mortality, but we observed a slight increase rather than a reduction in growth. Although this difference was not significant, it may suggest an antibiotic effect of OTC.

In the lower Columbia River, sublegal-length white sturgeons form an annulus by July. The period of annulus formation for populations at other latitudes may be quite different. We recaptured only two spawning-sized fish. Further investigation may demonstrate a different timing among mature fish. However, this source of error is most critical among young fish, for which a consistent bias of ± 1 year can greatly affect recruitment estimates. We observed some fin rays without annuli in July and August, but these may be fish that failed to form a detectable annulus during that year. Accuracy of aging could be reduced by failure to consider this period of annulus formation because annuli at the edge are difficult to distinguish (Sheri and Power 1969; Crawford et al. 1989). In the lower Columbia, collection of fin ray samples before May and after July will improve accuracy of interpretation.

Counts of translucent zones on white sturgeon pectoral fin rays underestimate age. Accuracy of age interpretation is related to growth rate: fish that grow slowly do not appear to form a detectable growth zone every year. Accuracy of age assignments declines with increasing size and age as fish live through more periods of reduced growth. Most fish we examined were less than 100 cm long, which is substantially smaller than the 164–194 cm reported for size at first spawning for female white sturgeons in these reservoirs (Welch and Beamesderfer 1993). Aging of spawning-sized

fish may be further complicated by crowding of annuli associated with reduced growth prior to spawning (Roussow 1957; Guénette et al. 1992; Keenlyne and Jenkins 1993) or by spawning checks (Sokolov and Malutin 1978).

We have shown that tagged white sturgeons from impounded reaches of the Columbia River grow substantially slower than the 10 cm/year expected for similar-sized fish in the free-flowing reach below these impoundments (DeVore et al. 1992). It is clear the potential for underaging white sturgeons from impounded reaches is great. Oregon, Washington, and tribal fishery managers have taken steps to reduce white sturgeon exploitation rates as well as the number of exploited age-classes in these impoundments by narrowing the slot limit, reducing daily and seasonal bag limits for sport anglers, and setting reservoir-specific harvest quotas for commercial fishers. The uncertainty in age assignments further justifies conservative regulation of fisheries in these impoundments.

Sustainable exploitation and yield of white sturgeon are sensitive to growth and natural mortality rates (Rieman and Beamesderfer 1990). Underestimates of age lead to overestimates of growth and natural mortality rates (Leaman and Nagtegaal 1987; Casey and Natanson 1992). The likely result of underaging from pectoral fin rays is that the sustainable exploitation rate for reservoirs of the Columbia River has been overestimated. Overestimates of annual growth may account for observed delays in recruitment of white sturgeon to recreational fisheries below Columbia River impoundments following a 10-cm increase in the minimum size limit in April 1989. Given the estimated growth rate of sublegal sturgeons, catch rates of legal-sized fish did not recover in 1991 as expected (Melcher and King 1992; S. King, Oregon Department of Fish and Wildlife, personal communication).

Ages determined from white sturgeon pectoral fin rays are not precise and underestimate the true age of larger fish. Despite these problems with aging, estimates based on fin ray sections may be compared among populations if biases can be assumed to be similar. Recent advances in aging otoliths with break-and-burn methodology (Chilton and Beamish 1982) have provided a more accurate alternative for aging for many long-lived species. Although otoliths have been used to age lake sturgeon *Acipenser fulvescens* (Harkness 1923; Schneberger and Woodbury 1944), they were reported difficult to process and read for white sturgeons due to their brittleness and asymmetric,

"lumpy" growth patterns (Brennan and Cailliet 1989; G. M. Cailliet, Moss Landing Marine Laboratories, personal communication). Other new methods, including radiometric dating and evaluation of stable isotopes, may prove useful (Cailliet and Tanaka 1990). However, the fin ray method remains the most useful method for aging live sturgeons. Even if otolith techniques prove useful, they require killing the fish. Until alternatives are developed to determine ages of white sturgeons, interpretations based on pectoral fin ray sections should be applied with caution.

Acknowledgments

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