Transactions of the American Fisheries Society 132:895–903, 2003

Growth Estimates from Tagged White Sturgeon Suggest That Ages from Fin Rays Underestimate True Age in the Kootenai River, USA and Canada

VAUGHN L. PARAGAMIAN*
Idaho Department of Fish and Game, 2750 Kathleen Avenue,
Coeur d'Alene Idaho 83815, USA

RAYMOND C. P. BEAMESDERFER
S. P. Cramer and Associates, Inc., 39330 Proctor Boulevard, Sandy, Oregon 97055, USA

Abstract.—We used tagging data for 760 recaptured Kootenai River white sturgeon *Acipenser transmontanus* that had been at large for as long as 23 years to examine the validity of ages assigned from pectoral fin rays. Growth estimates from tagged white sturgeon in the Kootenai River indicated that age estimates from fin rays were underestimates of the true ages. Bias was estimated from growth differences between length-at-age relationships derived from fin ray ages and recaptures of tagged fish. Growth of tagged fish was substantially less than predicted from fin ray length-at-age curves. Age-specific lengths estimated from fin rays cannot be achieved at the growth increments observed for tagged fish. Ages estimated from fin rays were 30–60% less than the apparent ages from tagging data. Thus, actual ages may be 1.5–2.0 times the ages estimated from fin rays. Apparent aging bias will result in substantial changes in population parameters estimated from age, including growth, mortality, longevity, and year-class strength, which will have significant implications for efforts to preserve this endangered species and enable it to recover.

Accurate age assessments are crucial for understanding and managing long-lived species such as sturgeon. When compounded over many years, even small aging errors may have large effects on estimates of growth rate, mortality rate, age of maturation, spawning periodicity, reproductive potential, year-class strength, and population productivity (Archibald et al. 1983; Beamish and McFarlane 1983; Bradford 1991; Richards et al. 1992). These population parameters often underlie assumptions of management models used to evaluate protection and recovery measures for weak stocks of sturgeon (Kincaid 1993; Morrow et al. 1999; Secor and Waldman 1999; Pine et al. 2001) and sustainable fishing rates for strong sturgeon stocks (Rieman and Beamesderfer 1990; Boreman 1997; Quist et al. 2002). Risks of demographic extinction or overfishing will be exacerbated by erroneous assumptions biased by aging error.

Sturgeon are commonly aged by counting the opaque and translucent banding patterns in thin cross sections of the leading pectoral fin ray, on the assumption that an annulus is laid down for each year of life (Currier 1951; Kohlhorst et al. 1980; Guénette et al. 1992; LeBreton and Beamish 2000). Fin ray sections have provided the greatest reader precision in evaluations of a variety of calcified age structures (Brennan and Caillet 1989) and can be removed with minimal harm to sturgeon (Rien et al. 1994; Collins and Smith 1996).

Although Beamish and McFarlane (1983) highlighted the need for validation of aging methods in fisheries biology, validation studies for sturgeon have been limited. Brennan and Caillet (1991) concluded that bands occurred annually based on results for oxytetracycline (OTC)-marked fin rays for 19 white sturgeon *Acipenser transmontanus* at large from 1 to 3 years. Rossiter et al. (1995) observed a close correspondence between the number of additional annuli and the number of years at large for paired fin samples and OTC-marked lake sturgeon *A. fulvescens* at large for 1–3 years but also noted that the close proximity of some annular rings could result in an underestimation of true age if two rings are counted as one. Sokolov and Akimova (1977) and Sokolov and Malyutin (1978) suggested that Siberian sturgeon *A. baeri* in the Lena River may form two bands per year and thus their ages could be overestimated. However, Rien and Beamesderfer (1994) observed consistent underestimation of years at large for impounded white sturgeon populations in the Columbia River, based on observations of 216 OTC-marked fish at large for 1–4 years.

Our objective was to use tagging data for Koote-

---

* Corresponding author: vparagam@idfg.state.id.us

Received September 27, 2002; accepted January 28, 2003

TABLE 1.—Release and recapture numbers for wild white sturgeon sampled in the Kootenai River, 1977–2001.

Year and catch variable	Number tagged	Year										
		1978	1979	1980	1981	1982	1983	1986	1987	1989	1990	1991
1977	96	0	0	0	1	1	1	0	0	1	1	0
1978	49		1	2	2	1	0	0	0	1	1	0
1979	19			2	0	1	0	0	0	0	0	0
1980	163				18	10	0	0	0	5	4	3
1981	156					7	1	0	0	7	0	1
1982	63						0	0	0	7	1	0
1983	10							0	0	0	0	0
1984	0							0	0	0	0	0
1985	0							0	0	0	0	0
1986	2								0	0	0	0
1987	10									1	0	0
1988	0									0	0	0
1989	208										23	6
1990	100											3
1991	43											
1992	44											
1993	81											
1994	133											
1995	178											
1996	105											
1997	60											
1998	69											
1999	39											
2000	50											
2001	26											
Total	1,704	0	1	4	21	20	2	0	0	22	30	13
Total catch		49	20	167	177	83	12	2	10	230	130	56
% Tagged		0	5	2	12	24	17	0	0	10	23	23

[a] Recaptured more than once.

nai River white sturgeon at large for as long as 23 years to examine the validity of ages assigned from pectoral fin rays and to quantify the apparent bias in age estimates. Predicted growth increments were estimated for each tagged fish from length-at-age curves based on length at tagging and years at large (von Bertalanffy's growth curve; Ricker 1975). Predicted increments were compared with observed increments between tagging and recapture to evaluate the accuracy of length-at-age relationships based on fin rays.

The Kootenai River white sturgeon is an isolated headwaters population that is listed as endangered under the U.S. Endangered Species Act (Duke et al. 1999; USFWS 1999). Natural recruitment has failed and the population now consists of a dwindling number of adults (Paragamian and Kruse 2001; Paragamian et al. 2001). Recovery measures include attempts to restore habitat conditions suitable for recruitment and instituting a conservation hatchery program (Paragamian et al. 2001; Ireland et al. 2002a, 2002b). Any discrepancies in age determinations could have serious consequences for demographic studies and recovery measures.

Methods

Mark–recapture data are available for Kootenai River white sturgeon sampled in many unpublished studies from 1978 through 2001 and on file with the Idaho Department of Fish and Game (IDFG; Panhandle Region, Coeur d' Alene, Idaho). Individual fish were distinguished with uniquely numbered spaghetti or passive integrated transponder (PIT) tags. Fork length (FL) was recorded to the nearest centimeter at release and recapture. Pectoral fin ray sections were collected from many fish and subsequently used to estimate age using standard methods (Brennan and Caillet 1989). All fin ray sections were aged by at least two experienced viewers. All data were standardized in a comprehensive database maintained by the IDFG.

The validity of ages assigned from pectoral fin rays was inferred on the basis of a comparison of the observed growth increments from length-at-age curves and recaptures of marked fish to develop predicted lengths at age. Length-at-age curves were fit to fin ray age data by using von Bertalanffy's (Ricker 1975) equation and a non-

TABLE 1.—Extended.

Year and catch variable	Year											Recapture rate	
	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	Total	Average	Individuals[a]
1977	0	0	1	0	0	0	1	0	1	0	8	0.3	6.3
1978	0	0	2	0	0	0	0	1	0	0	11	1.0	16.3
1979	0	0	0	0	0	0	0	0	0	0	3	0.7	15.8
1980	1	2	3	4	7	4	4	1	2	1	69	2.0	23.9
1981	1	0	7	2	2	1	2	2	2	1	36	1.2	14.7
1982	0	3	3	3	1	7	4	3	4	3	39	3.3	23.8
1983	0	1	1	1	0	0	0	0	0	0	3	1.7	30.0
1984	0	0	0	0	0	0	0	0	0	0	0	5.9	0.0
1985	0	0	0	0	0	0	0	0	0	0	0	6.3	0.0
1986	0	0	1	0	0	0	0	0	0	0	1	3.3	50.0
	1	0	1	0	1	1	0	0	1	0	6	4.3	40.0
1987	0	0	0	0	0	0	0	0	0	0	0	7.7	0.0
1988	6	13	18	28	14	15	15	17	10	12	177	7.1	46.6
1089	7	6	8	11	9	12	10	5	6	10	87	7.9	45.0
1090	2	2	6	4	2	4	2	3	6	1	32	7.4	41.9
1091		1	3	4	3	1	1	3	3	1	20	5.1	31.8
1092			4	12	6	3	8	3	9	2	47	7.3	37.0
1093				11	12	2	13	7	10	6	61	6.6	32.3
1094					18	10	21	14	16	9	88	8.2	33.7
1095						7	8	8	10	7	40	7.6	24.8
1996													
1197							7	2	5	5	19	7.9	25.0
1198								1	4	2	7	3.4	10.1
1999									2	4	6	7.7	12.8
2000										0	0	0.0	0.0
2001											0	0.0	0.0
Total	18	28	58	80	75	67	96	70	91	64	760		27.1
Total catch	62	110	193	258	180	127	165	109	141	90	3,271		
% Tagged	29	25	30	31	42	53	58	64	65	71	23		

linear curve-fitting routine. Predicted annual growth increments of tagged individuals were calculated as the difference between length at release after tagging and lengths after recapture, divided by years at large.

Length-at-age curves were derived from tagging data with a modification of the method of Fabens (1965). Growth increment data were fitted to a von Bertalanffy growth curve reformulated in terms of size increments versus size at tagging and period at large, namely,

$$\Delta L = (L_\infty - L_t)(1 - e^{-kT})$$

where t is time of tagging, T is the number of years between tagging and recapture, ΔL is the increase in length between release and recapture ($L_{t+T} - L_t$), L_∞ is the von Bertalanffy length at infinity, and k is the von Bertalanffy growth rate coefficient. We estimated L_∞ and k by using a linear regression of growth increment versus length where the slope was equal to $e^{-k} - 1$ and the x-intercept was L_∞ (Gulland 1983; Haddon 2001). To standardize data for various periods at large, we annualized the growth increment ($\Delta L/T$) and expressed length as the median between tagging and recapture ($[L_{t+T} + L_t]/2$). Since this method does not provide an independent estimate of the hypothetical age at which fish would have been zero length (t_0), found in the von Bertlanffy equation, we used the estimate based on the fin ray regression for both length-at-age curves.

Bias in age estimated from fin rays was quantified by using comparisons of observed length-at-age curves from fin rays and tagging data. Age (t) for fish of any given size (L_t) was estimated by another reformulation of the von Bertalanffy equation (Kirkwood 1983):

$$t = t_0 \text{—} \log_e[(1 \text{—} L_t/L_\infty)/k]$$

The apparent average age was estimated with parameters derived from tagging data. Apparent ages were compared with corresponding average ages for fish of the same length as based on fin ray data growth curves. The apparent bias in the fin ray aging method was expressed as the difference in actual versus predicted age relative to the actual age.

Results

Of the total of 1,704 Kootenai River white sturgeon that were marked from 1977 through 2001

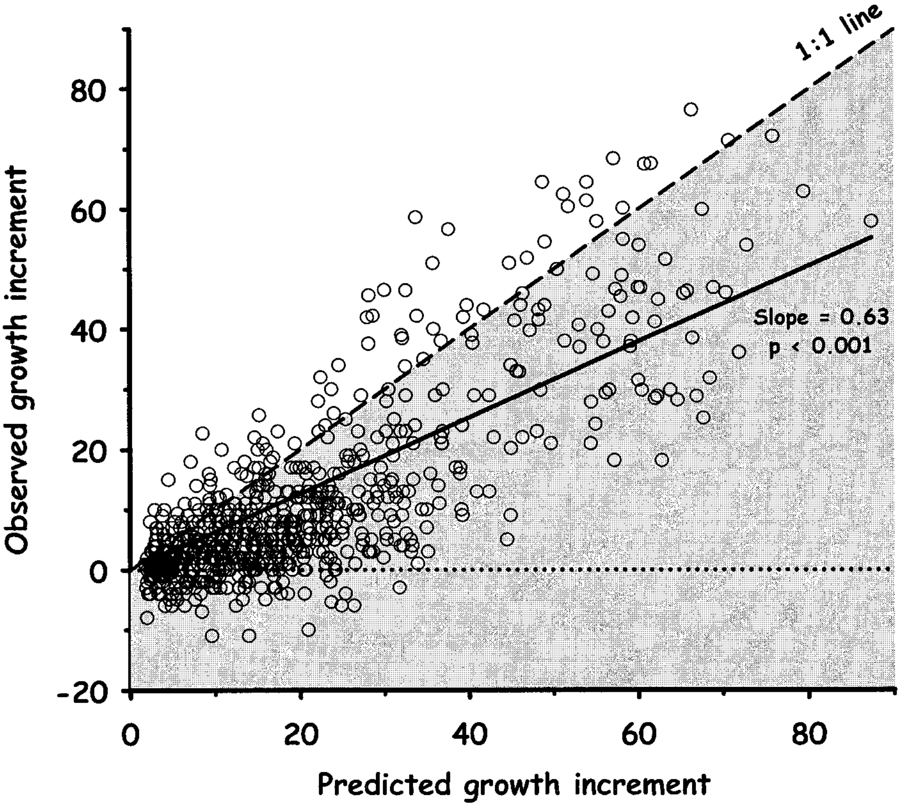

FIGURE 1.—Comparison of the growth increments of Kootenai River white sturgeon observed between tagging and recapture with the average growth increments predicted by the length-at-age relationship derived from fin ray aging. The predicted increments were based on length at tagging and the number of years at large.

and at large for up to 23 years, we examined the length and age records of the 760 that were recaptured (Table 1). Some Kootenai River white sturgeon were recaptured as much as six times each during this period. Individual recaptures by year of tagging were as great as 50% and averaged 27%.

The growth of the tagged fish (n = 737; 23 records were not usable) was substantially less than the increments predicted by length-at-age relationships derived from fin ray ages (Figure 1). Observed growth rates fell well below a 45° line, indicating a discrepancy between observed and predicted growth increments.

Growth rates of tagged fish averaged 2.76, 1.47, and 0.57 cm per year for small, medium, and large white sturgeon (Figure 2). In contrast, the annual growth increments of the same size-classes predicted from the fin ray age-at-length function were 3.8–4.9, 3.2–3.7, and 1.3–3.1 cm per year, respectively. Differences between fin ray aging and tagging estimates were reflected in plots of length versus age (Figure 3) and of growth increment versus fork length (Figure 4). Growth curves and annual growth increments were substantially less for the mark–recapture method than for the fin ray method.

Ages estimated from fin rays were 30–60% less than apparent ages from tagging data, the size of the estimated error increasing with age (Figure 5). These errors correspond to apparent ages that were 1.5–2.0 times the ages estimated from fin rays.

Discussion

Length-at-age functions such as that of von Bertalanffy infer growth rates from age data. We inferred age from growth rate data and attributed all differences between fin ray and tagged fish growth to errors in fin ray aging. Age-specific lengths estimated from fin rays cannot be achieved at the growth increments observed for tagged fish. This discrepancy suggests that ages assigned from fin rays are substantial underestimates for Kootenai River sturgeon.

This approach assumed that the growth rates of

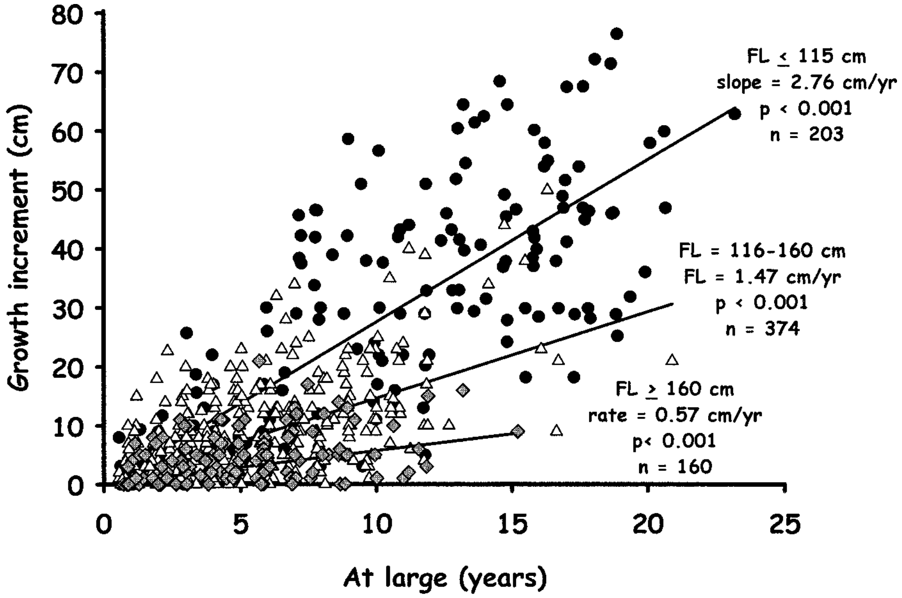

FIGURE 2.—Observed growth increments of tagged Kootenai River white sturgeon relative to years at large, by length-class (circles = ≤115 cm, open triangles = 166−160 cm, and gray triangles ≥160 cm).

Kootenai River white sturgeon did not change substantially over time. Length-at-age estimates reflect the growth conditions that preceded those represented by tagging estimates. Aging bias would be less than our estimates if recent growth rates were less than historic rates. However, no temporal changes in growth rate are apparent for length-at-age data from fin rays (Young 2002), despite changes in Kootenai River water temperature and productivity associated with upstream reservoir construction and control of industrial effluents (Woods 1982; Knudson 1994; Snyder and Minshall 1995; Paragamian et al. 2001). Young (2002) concluded that the complex series of biotic and

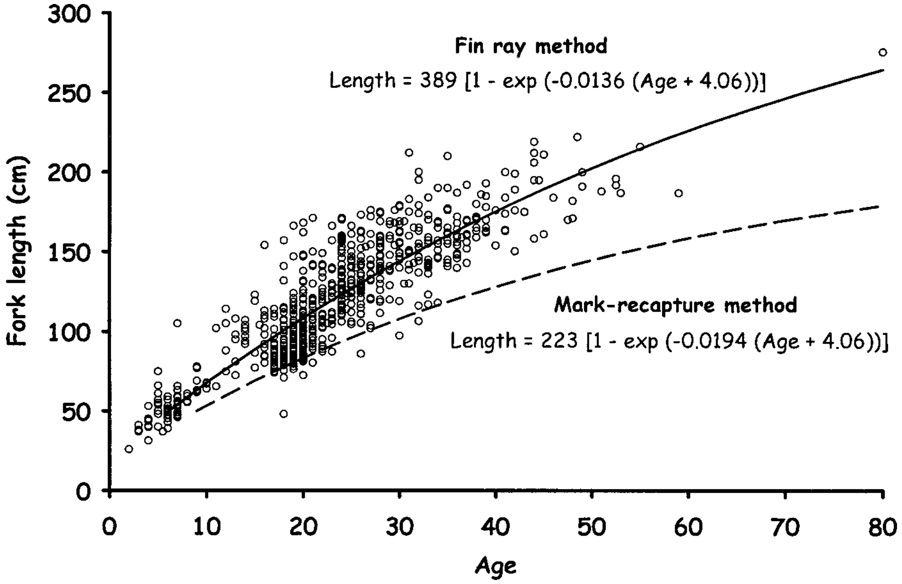

FIGURE 3.—Length at age of Kootenai River white sturgeon based on fin ray samples collected from 1978 to 2001. The length-at-age relationship derived from tagging data is included for comparison.

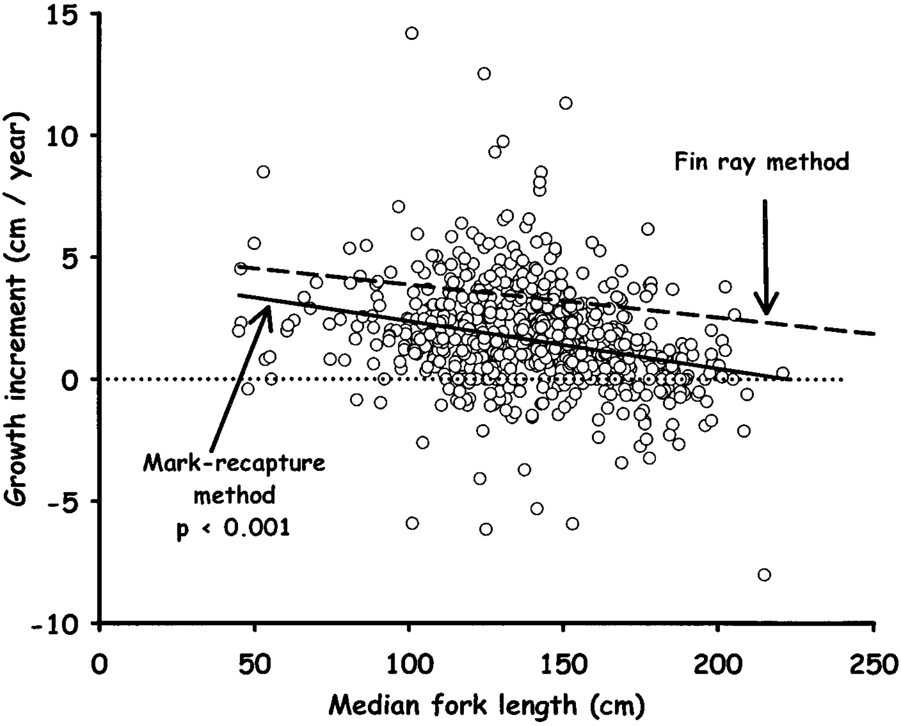

FIGURE 4.—Average annual growth increment versus median fork length between tagging and recapture of Kootenai River white sturgeon collected from 1978 to 2001. The corresponding length-at-age relationship derived from fin ray samples is included for comparison.

abiotic interactions associated with the decline of Kootenai River white sturgeon has not been expressed in slower growth rates. In addition, C. Spence (Rare and Threatened Fisheries Biologist, British Columbia Ministry of Water, Land, and Air Protection) examined the Fulton condition factor of Kootenai River white sturgeon, captured in Kootenay Lake, during pre- and postfertilization of Kootenay Lake and could find no difference between the two periods.

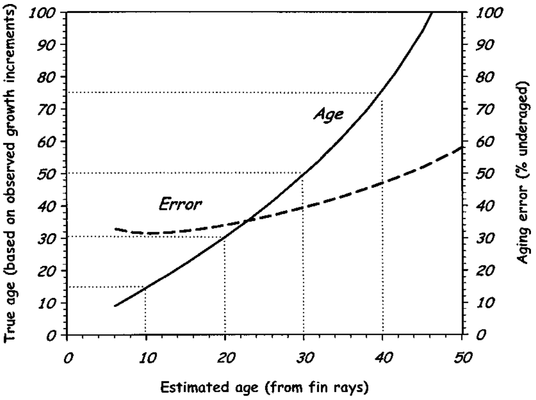

FIGURE 5.—Relationship between ages estimated from fin rays and those from tagging data, with the corresponding age-specific errors (difference divided by true age).

Our approach to estimating aging error also assumed no compounding effects of the different approaches used to derive length at age. Fin ray samples provide direct estimates of length at age. Fabens' method describes individual growth based on tagging data but does not explicitly predict average length at a given age (Sainsbury 1980; Francis 1995). Several authors caution that von Bertalanffy parameters generated from size-at-age data have been given different interpretations from those generated from tagging data because the curves are being fitted by using very different residual error structures (Kirkwood 1983; Maller and deBoer 1988; Francis 1995; Haddon 2001). The estimation of L_∞ tends to be biased upwards from tagging data with a corresponding decrease in the k parameter (Haddon 2001). However, our analysis uses parameter estimates to describe growth increments and does not explicitly compare growth function parameters. Bias in individual L_∞ and k

is overcome by considering parameter estimates jointly (Sainsbury 1980).

Apparently, aging problems of fin rays are not unique to the Kootenai River white sturgeon population but may also occur in other white sturgeon populations and sturgeon species (Sokolov and Akimova 1977; Sokolov and Malyutin 1978; Rien and Beamesderfer 1994). Slow growth rates of this isolated headwater population may magnify problems. Beamesderfer (1993) reported much poorer condition factors for Kootenai River white sturgeon than for other populations in Idaho, Washington, Oregon, California, and British Columbia. On the basis of fin ray length-at-age estimates, Kootenai River white sturgeon average 110 cm FL at age 20. In contrast, white sturgeon in lower Columbia River populations average 120–140 cm FL at age 20 (Beamesderfer et al. 1995). Population growth differences might account for the discrepancy between Kootenai River white sturgeon, where fin ray ages were underestimates, and Sacramento–San Joaquin River white sturgeon, where Brennan and Caillet (1991) reported OTC results consistent with annual banding.

Accurate assessments of status and population dynamics are crucial for the preservation and recovery of Kootenai River white sturgeon, and errors in population parameter estimation may have serious implications. The aging bias of fin rays translates into biases in other population parameters estimated from age. Kootenai River white sturgeon live longer, suffer less annual mortality, grow more slowly, and mature later than previously thought. The effects of these interacting changes on population dynamics are complex. On the one hand, fish live longer and mortality rates may be less than previously thought. However, growth is much slower and maturation probably occurs at older ages.

Comparisons of growth rates estimated from anatomical structures and tagging data are an indirect but useful method of validating age estimates where fish of known ages are not available. This approach differs from the conventional mark–recapture age validation approach, which involves comparison of ages from hard parts removed at tagging and recapture or use of fluorochrome labels such as OTC (Beamish and McFarlane 1983). Other alternatives, including microelemental analysis, may not be appropriate for sturgeon because of their unique cartilaginous physiology (Veinott and Evans 1999). Although our use of a growth inferential validation method identified the potential for significant biases in fin ray age estimates, this conclusion should be corroborated with further studies of fin ray aging for fish of known ages. Collection of a second fin ray sample from marked fish that were aged previously is one alternative for the near term. An OTC marking program is another alternative. Future collection of fin rays of known-age hatchery fish released from the hatchery as juveniles (Ireland et al. 2002b) and individually marked with PIT tags will help resolve aging questions over the long term.

Acknowledgments

We thank previous IDFG Kootenai River researchers Fred Partridge, Kim Apperson, Pat Marcuson, Gretchen Kruse, and Vint Whitman for their collection of fin rays and age analysis. We also thank Jack Siple of the Kootenai Tribe of Idaho (KTOI) for the collection of fin ray samples and Robert Lindsey and Colin Spence of the British Columbia Ministry of Land, Water, and Air Protection for their cooperative efforts in fin ray collections and age analysis. Diane Wakkinen of IDFG maintained the database. Thanks to Sue Ireland of the KTOI for her support and administration of the main body of funding for this investigation. Colin Chapman assisted with data summary and presentation. Steve Yundt and Pete Rust of IDFG provided editorial comments. Tom Rien provided helpful observations and comments. The Bonneville Power Administration, IDFG, and the KTOI provided funding for this work. Thanks also to the Bonneville Power Administration for additional funding.

References

Archibald, C. P., D. Fournier, and B. M. Leaman. 1983. Reconstruction of stock history and development of rehabilitation strategies for Pacific Ocean perch in Queen Charlotte Sound, Canada. North American Journal of Fisheries Management 7:138–141.

Beamesderfer, R. C. 1993. A standard weight (Ws) equation for white sturgeon. California Fish and Game 79:63–69.

Beamesderfer, R. C., T. A. Rien, and A. A. Nigro. 1995. Differences in the dynamics and potential production of impounded and unimpounded white sturgeon populations in the lower Columbia River. Transactions of the American Fisheries Society 124:857–872.

Beamish, R. J., and G. A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 112:735–743.

Boreman, J. 1997. Sensitivity of North American sturgeon and paddlefish populations to fishing mortality. Environmental Biology of Fishes 48:399–405.

Bradford, M. J. 1991. Effects of ageing errors on recruitment time series estimated from sequential population analysis. Canadian Journal of Fisheries and Aquatic Sciences 48:555–558.

Brennan, J. S., and G. M. Caillet. 1989. Comparative age-determination techniques for white sturgeon in California. Transactions of the American Fisheries Society 118:296–310.

Brennan, J. S., and G. M. Caillet. 1991. Age determination and validation studies of white sturgeon, *Acipenser transmontanus*, in California. Pages 209–234 *in* P. Williott, editor. *Acipenser*. Centre National du Machinisme Agricole du Genie Rural des Eaux et des Forets, Bordeaux, France.

Collins, M. R., and T. I. J. Smith. 1996. Sturgeon fin ray removal is nondeleterious. North American Journal of Fisheries Management 16:939–941.

Currier, J. P. 1951. The use of pectoral fin rays for determining age of sturgeon and other species of fish. Canadian Fish-Culturist 11:10–18.

Duke, S., P. Anders, G. Ennis, R. Hallock, J. Hammond, S. Ireland, J. Laufle, R. Lauzier, L. Lockhard, B. Martoz, V. L Paragamian, and R. Westerhof. 1999. Recovery plan for Kootenai River white sturgeon (*Acipenser transmontanus*). Journal of Applied Ichthyology 15:157–163.

Fabens, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

Francis, R. I. C. C. 1995. An alternative mark-recapture analogue of Schnute's growth model. Fisheries Research 23:95–111.

Guénette, S., D. Goyette, R. Fortin, J. Leclerc, N. Fournier, G. Roy, and P. Dumont. 1992. La periodicite de la croissance chez la femelle de l'esturgeon jaune (Acipenser fulvescens) du fleuve Saint-laurent Estelle reiee a la periodicite de la reproduction? [Is growth periodicity of the female lake sturgeon (*Acipenser transmontanus*) of the St. Lawrence River related to production periodicity?] Canadian Journal of Fisheries and Aquatic Sciences 49:1336–1342.

Gulland, J. A. 1983. Fish stock assessment: a manual of basic methods. Wiley, New York.

Haddon, M. 2001. Modeling and quantitative methods in fisheries. Chapman and Hall/CRC, Boca Raton, Florida.

Ireland, S. C., P. J. Anders, and J. T. Siple. 2002a. Conservation aquaculture: an adaptive approach to prevent extinction of an endangered white sturgeon population. Pages 211–222 *in*, W. V. Winkle, P. Anders, D. H. Secor, and D. Dixon, editors. American Fisheries Society, Symposium 28, Bethesda, Maryland.

Ireland, S. C., J. T. Siple, R. C. P. Beamesderfer, V. L. Paragamian, and V. D. Wakkinen. 2002b. Success of hatchery-reared juvenile white sturgeon (*Acipenser transmontanus*) following release in the Kootenai River, Idaho. Journal of Applied Ichthyology 18:642–650.

Kincaid, H. 1993. Breeding plan to preserve the genetic variability of the Kootenai River white sturgeon. U.S. Fish and Wildlife Service, Report to the Bonneville Power Administration, Project 93–27, Wellsboro, Pennsylvania.

Kirkwood, G. P. 1983. Estimation of von Bertalanffy growth curve parameters using both length increment and age-length data. Canadian Journal of Fisheries and Aquatic Sciences 40:1405–1411.

Knudson, K. 1994. Water quality status report: Kootenay River basin British Columbia, Montana, and Idaho. Ecological Resource Consulting, Report to the Kootenai River Network, Libby, Montana.

Kohlhorst, D. W., L. W. Miller, J. J. Orsi. 1980. Age and growth of white sturgeon collected in the Sacramento-San Joaquin estuary, California: 1965–1970 and 1973–1976. California Fish and Game 66: 83–95.

LeBreton, G. T. O., and F. W. H. Beamish. 2000. Suitability of lake sturgeon growth rings in chronology development. Transactions of the American Fisheries Society 129:1018–1030.

Maller, R. A., and E. S. deBoer. 1988. An analysis of two methods of fitting the von Bertalanffy curve to capture-recapture data. Australian Journal of Freshwater Research 39:459–466.

Morrow, J. V., Jr., J. P. Kirk, K. J. Kilgore, and H. E. Rogillio. 1999. Recommended enhancements to the gulf sturgeon recovery and management plan based on Pearl River studies. North American Journal of Fisheries Management 19:1117–1121.

Paragamian, V. L., and G. Kruse. 2001. Kootenai River white sturgeon spawning migration behavior and a predictive model. North American Journal of Fisheries Management 21:10–21.

Paragamian, V. L., G. Kruse, and V. Wakkinen. 2001. Spawning habitat of Kootenai River white sturgeon, post-Libby Dam. North American Journal of Fisheries Management 21:22–33.

Pine, W. E., III, M. S. Allen, and V. J. Dreitz. 2001. Population viability of the Gulf of Mexico sturgeon: inferences from capture-recapture and age-structured models. Transactions of the American Fisheries Society 130:1164–1174.

Quist, M. C., C. S. Guy, M. A. Pegg, P. J. Braaten, C. L. Pierce, and V. H. Travnichek. 2002. Potential influence of harvest on shovelnose sturgeon populations in the Missouri River system. North American Journal of Fisheries Management 22:537–549.

Richards, L. J., J. T. Schnute, A. R. Kronlund, and R. J. Beamish. 1992. Statistical models for the analysis of ageing error. Canadian Journal of Fisheries and Aquatic Sciences 49:1801–1815.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Rieman, B. E., and R. C. Beamesderfer. 1990. White sturgeon in the lower Columbia River: is the stock overexploited? North American Journal of Fisheries Management 10:388–396.

Rien, T. A., and R. C. Beamesderfer. 1994. Accuracy and precision of white sturgeon age estimates from pectoral fin rays. Transaction of the American Fisheries Society 123:255–265.

Rien, T. A., R. C. P. Beamesderfer, and C. F. Foster. 1994. Retention, recognition, and effects on survival of several tags and marks on white sturgeon.

California Department of Fish and Game 80:161–170.

Rossiter, A., D. L. G. Noakes, and F. W. H. Beamish. / 1995. Validation of age estimation for the lake sturgeon. Transactions of the American Fisheries Society 124:777–781.

Sainsbury, K. J. 1980. Effect of individual variability on the von Bertalanffy growth equation. Canadian Journal of Fisheries and Aquatic Sciences 37:241–247.

Secor, D. H., and J. R. Waldman. 1999. Historical abundance of Delaware Bay Atlantic sturgeon and potential rate of recovery. Pages 203–216 *in* J. A. Musick, editor. Life in the slow lane: ecology and conservation of long-lived marine animals. American Fisheries Society, Symposium 23, Bethesda, Maryland.

Snyder, E. B., and G. W. Minshall. 1995. Ecosystem metabolism and nutrient dynamics in the Kootenai River in relation to impoundment and flow enhancement for fisheries management. Idaho State University, Stream Ecology Center, Progress report, Pocatello.

Sokolov, L. I., and N. V. Akimova. 1977. Age determination of the Lena River sturgeon *Acipenser baeri*. Journal of Ichthyology 16:773–778.

Sokolov, L. I., and V. S. Malyutin. 1978. Features of the podpulation structure and characteristics of spawners of the Siberian sturgeon, *Acipenser baeri*, in the spawning grounds of the Lena River. Journal of Ichthyology 17:210–218.

USFWS (U.S. Fish and Wildlife Service). 1999. Recovery plan for the Kootenai River population of the white sturgeon (*Acipenser transmontanus*). USFWS, Region 1, Portland, Oregon.

Veinott, G. I., and R. D. Evans. 1999. An examination of elemental stability in the fin ray of white stugeon with laser ablation sampling—inductively coupled plasma—mass spectophotometry (LAS-ICP-MS). Transactions of the American Fisheries Society 128: 352–361.

Woods, P. F. 1982. Annual nutrient loadings, primary productivity, and trophic state of Lake Koocanusa, Montana and British Columbia, 1972–80. U.S. Geological Survey, Professional Papers 1283.

Young, W. 2002. Juvenile habitat use and growth of the Kootenai River white sturgeon. Master's thesis. University of Idaho, Moscow.