Kootenai River Juvenile White Sturgeon Population Analyses

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FINAL REPORT

February 2015

Subcontract for Kootenai River Resident Fish Mitigation Program

BPA Contract # 1988-065-00

Subcontract Tracking # IDFG-FY14-266

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White Sturgeon (*Acipenser transmontanus*) have been reintroduced into the Kootenai River system of Idaho, Montana, and British Columbia (BC) since 1992 (Paragamian and Beamesderfer 2004). Due to geographic isolation, declining abundance, and ongoing recruitment failure, the population was listed as endangered in the U.S. under the Endangered Species Act (ESA) in 1994 (Duke at al. 1999, Paragamian et al. 2005, USFWS 2006), and in British Columbia under the Canadian Species at Risk Act in 2007. Although the specific causes of recruitment failure remain unclear, research to date suggests that egg and/or larval suffocation, predation, and/or other factors of early life mortality contribute to persistent recruitment failure (Kock et al. 2006). The Kootenai River White Sturgeon population is comprised mainly of old adults, and significant recruitment has not occurred since the 1970s. Until recruitment failure can be addressed through habitat enhancement or other mitigation efforts, this species will only survive with the aid of conservation aquaculture (Paragamian and Beamesderfer 2004). The reliance on hatchery-reared fish to maintain this population has prompted a need for detailed information on population size, annual survival, and the influence of specific release strategies.

Study Area

The Kootenai River originates in Kootenay National Park, BC, Canada. The river flows south into Montana and turns northwest at Jennings, near the site of Libby Dam, at river kilometer (rkm) 352.4 (Figure 1). River kilometers were defined as the upstream distance (in kilometers) from the northern most reach of Kootenay Lake. Kootenai Falls, located 42 rkms downstream from Libby Dam, may be an impassable barrier to White Sturgeon, along with other fish species. As the river flows through the northeast corner of Idaho, there is a gradient transition at Bonners Ferry. Upstream from Bonners Ferry, the channel has an average gradient of 0.6 m/km, and the velocities are often higher than 0.8 m/s. Downstream from Bonners Ferry, the river slows to velocities typically less than 0.4 m/s (average gradient of 0.02 m/km), and the channel deepens as the river meanders north through the Kootenai River valley. The river returns to BC at rkm 170 and enters the South Arm of Kootenay Lake at rkm 120. The river leaves the lake through the West Arm of Kootenay Lake (rkm 76) and flows to its confluence with the Columbia River at Castlegar, BC. A natural barrier at Bonnington Falls (now a series of four dams) has isolated the Kootenai River White Sturgeon from other populations in the Columbia River basin for approximately 10,000 years (Northcote 1973). The entire Kootenai River basin drains an area of 49,987 km^2 (Bonde and Bush 1975). Regulation of the Kootenai River following the construction of Libby Dam in 1974 changed the natural hydrograph and temperatures of the river, which has had lasting effects on White Sturgeon and other fish species in the river (Partridge 1983).

METHODS

The specific objectives of these data analyses were to:

1. Make sampling recommendations to meet population closure assumptions needed to estimate population size.
2. Provide updated estimates of annual survival as a function of age class.
3. Investigate the influence of individual covariates and hatchery source on annual survival.
4. Replicate a virtual population analysis to estimate juvenile abundance by year similar to Beamesderfer et al. (2013).
5. Investigate effects on growth over time in this population using length-frequency data.

Juvenile White Sturgeon Sampling

Weighted, multifilament gill nets with 1.3, 1.9, 2.5, 3.8, 5.1, 6.4, and 7.6 cm stretch mesh were used to sample juvenile sturgeon. Sampling was conducted annually from 1992 to 2012 during July through October following the methodology of Paragamian et al. (1996). Gill nets were set during the daytime and checked every hour to reduce mortality, and all sturgeon were released alive. Upon capture, fork (FL) and total length (TL), weight, Passive Integrated Transponder (PIT) tag numbers, fish condition, and scute removal patterns were recorded for each sturgeon collected during gill netting efforts. Idaho Department of Fish and Game personnel sampled upstream of rkm 170 and BC Ministry of Forests, Lands and Natural Resource Operations (BCMFLNRO) personnel sampled from Kootenay Lake, BC to rkm 165.

From the years 1992 to 2004, prior to release, each hatchery reared sturgeon received a PIT tag and a pattern of scutes was removed at the Kootenai Tribe of Idaho (KTOI) hatchery located in Bonners Ferry, ID or at the Kootenay Trout and Sturgeon Hatchery located in Ft. Steele, BC. The Kootenay Trout and Sturgeon Hatchery is operated by the Freshwater Fishery Society of BC as the backup facility for the KTOI. Most (92%) of the released juvenile White Sturgeon were not PIT tagged from 2005 through 2007; however, scutes were removed from each fish prior to release, functionally serving as batch marks. Over 90% of the hatchery reared juvenile sturgeon released in the Kootenai River after 2007 were PIT tagged and all had scutes removed. Total numbers of hatchery releases are provided in Table 1. PIT tagging fish prior to release provided a unique identifier for each fish and allowed tracking of the size-at-release, rearing facility, release location, and time of release.

Closure Assumption

One objective of the Kootenai River White Sturgeon recovery efforts was to estimate the number of sturgeon in the system. Previous studies used differing methods and sets of assumptions to estimate abundance (Justice et al. 2009, Beamesderfer et al. 2013). One challenge of estimating population size is that it must be done under the assumption of population closure. The demographic closure assumption means that there cannot be births, deaths, immigration, or emigration occurring during the sampling period. In practice, this is difficult to achieve because sampling efforts for sturgeon present many logistical challenges and because recapture probabilities are low overall (Beamesderfer et al. 2013).

In summer 2013, researchers attempted a more intensive sampling effort than usual at two sites in BC (rkm 130 and 141) with the goal of using a closed capture model to estimate the abundance of juvenile sturgeon. Researchers sampled for three days at both sites using standard gill net sampling (Stephenson et al. 2014), with the goal of improving capture and recapture probabilities. This, in turn, would potentially allow the later use of a robust design analysis (Kendall et al. 1995) that could provide estimates of fish abundance and annual survival. To evaluate the closure assumption, closed captures model in Program MARK (White and Burnham 1999) were used to model capture and recapture probabilities and population abundance at each of the two sites.

Annual Survival

A dataset comprised of 21 years of capture and recapture data for the Kootenai River White Sturgeon was used for this analysis. The dataset required some initial “cleaning” with respect to assigning age-at-release to some fish, updating capture histories, and reconciling minor data entry errors. Thus, the final sample for use with these analyses was slightly different from the 125,948 used in Beamesderfer et al. (2013; Table 2).

After data cleaning, the capture and recapture information was summarized into an encounter history for each fish. The dataset consisted of 21 years (1992 to 2012), and fish were grouped into four age classes (age-1, age-2, age-3+, and Unknown age) with five individual covariates (Hatchery, Fork Length, Weight, Release Area, and Release Season) for analyses. In a small number of cases (<0.1% of the total) the individual covariate values were missing; for each such case the missing value was interpolated as the mean from the entire sample.

Annual age-specific survival was estimated using the live recaptures (Cormack-Jolly-Seber; CJS) model in Program MARK (White and Burnham 1999). The parameters in this model were annual apparent survival (ϕ) and conditional capture probability (p). With 21 years of data, this model yielded 20 estimates of annual survival and 20 estimates of capture probability.

Dependency in the data was tested for using the median c-hat procedure in MARK. The standard 120 simulations were run with no model failures, and c-hat was estimated as 1.31 from the global model. This adjustment was done in MARK and changed model selection from AIC to quasi-likelihood theory (QAICc), because c-hat was no longer assumed to equal the default value of 1.0 (Akaike 1973).

The modeling approach to estimate age-specific annual survival occurred in several steps, each to answer a specific question. The first step was to update the survival estimates in Beamesderfer et al. (2013) by using true age and not time-since-release. The Beamesderfer et al. (2013) analysis used the latter approach, but called this an “age” effect. For the analysis reported herein, the entire dataset was reformatted to code for true age effects. Beamesderfer et al. (2013) would have modeled the annual survival of a fish of any age-at-release as a function of time-since-release (one year, two years, etc.). The current analysis instead used all fish of a particular age (e.g., age-1 at-release) and modeled annual survival independently for each age class. Beamesderfer et al. (2013) modeled annual survival by release group, where a release group may have been comprised of more than one age class. Because age-0 fish were not individually marked, this age class was missing from these analyses. “Age-1” in this analysis matched up with the first year post-release (also age-1), “age-2” corresponded with the second year post-release, etc. As an initial comparison of age effects and time-since-release, the seven models in Table 1 of Beamesderfer et al. (2013) were re-analyzed; this provided a direct comparison of the model selection results and resulting estimates of annual survival and capture probability.

After the initial analysis was completed it became apparent that some of the survival and recapture parameters were either inestimable or were estimated very poorly because they were close to 0 or 1. This is a frequent problem in these types of analyses, and additional estimation procedures are sometimes required to obtain interpretable estimates. In this case, the Markov-Chain Monte Carlo (MCMC) tool in Program MARK (White and Burnham 1999) was used to resolve estimation problems in some age classes and years. The MCMC tool is computer intensive, so this was only used on the best model from the CJS analysis described above. In MARK the default settings (4,000 tuning samples, 2,000 burn-in samples, 10,000 iterations saved) were used to get parameter estimates, standard errors, and 95% credible intervals. A credible interval is akin to a 95% confidence interval, except that the limits are the 2.5% and 97.5% values from the posterior distribution of the parameter of interest.

Covariate Effects on Survival

Following the initial comparison of survival estimates to Beamesderfer et al. (2013), a more thorough analysis of the capture-recapture data was completed that incorporated additional covariate effects. The five covariates considered in the analysis were Hatchery, Fork Length, Weight, Release Area, and Release Season. Hatchery was coded as 1 = KT, -1 = BC, and 0 for an unknown hatchery. Fork length was measured at initial capture in cm and weight was measured at initial capture in kilograms; both were modeled only on the first year post-release because the value of each covariate was expected to change in subsequent years. Release area was designed to parse out differences by region and was coded as unknown (0), Kootenay Lake (1), Kootenay River in British Columbia (2), Kootenai River in Idaho below rkm 245 (3), Moyie River in Idaho (4), Leonia, Idaho/Montana (5), Yaak, Montana (6), and Troy, Montana (7) (Figure 1). Release area was not incorporated into the current analyses, but this could be explored later, if necessary. Finally, sturgeon were released under different strategies by season, and this covariate was coded as "0" for unknown, "1" for spring (March 20 – June 20), "2" for summer (June 21 – September 21), "3" for fall (September 22 – December 20), or "4" for winter (December 21 – March 19).

After completing the covariate analysis, the effect(s) of fork length on predicted survival of age-1 fish were cursorily evaluated. The mean value for a typical release from all hatcheries was calculated (25 cm) and used; age-specific annual survival of age-1 fish was predicted for a spring and fall release. Varying fork length within the spring release was also evaluated and annual survival for the mean (25 cm) in addition to small (20 cm) and large (30 cm) fish was predicted. This portion of the analysis was intended to provide additional insight into the possible effect(s) of releasing juvenile sturgeon during different seasons, at different fork lengths, and the interaction between these two variables.

Lastly, comments from external reviewers on an earlier version of this report raised questions about possible differences in the annual survival of age-2 fish as a function of whether they were released as age-1 fish and grew into this age class, or whether they were newly released at age-2 (i.e., did not grow into the age-2 class, in river). To address this question, year effects were added for 2001, 2002, and 2004 (the three years when age-2 fish were available in both scenarios) to the best model for annual survival.

Virtual Population Analysis

In general, the virtual population analysis of Beamesderfer et al. (2013) was replicated but with different estimates of annual survival. Importantly, for age-0 fish, annual survival was inestimable because none of the previously released age-0 fish were uniquely marked. Therefore, an annual age-0 survival rate of 0.0004 (derived from Gulf Sturgeon data; Pine et al. 2001) was used as a surrogate for age-0 survival. A deterministic, stage-based projection model was constructed to estimate the number of fish each year that were attributed to each release year. Numbers were then summed across age classes to obtain annual estimates of the sturgeon population. This approach had a few key assumptions that raised concerns during the analysis. Because there was some evidence that fish were mobile, even during short time periods (Neufeld and Rust 2009), the assumption of population closure under which population size was estimated was problematic. The model also used estimates of apparent survival (apparent survival was the product of true survival and fidelity), which may have been biased low if there was substantial permanent emigration from sampling sites. Lastly, these estimates were presented with an understanding that they were most informative of population processes when combined with other information on annual survival, recruitment, and dispersal.

RESULTS

Juvenile White Sturgeon Sampling

These analyses of annual survival of Kootenai River White Sturgeon incorporated capture and recapture information from 122,642 fish. These fish were released into the system at age-1 (107,995), age-2 (11,383), age-3+ (1,148), or an unknown age (2,116) (Table 1). Of this total, 69,807 were released from the BC hatchery, 50,521 were released from the KTOI hatchery, and 2,314 had an unknown hatchery source. The large dataset of capture and recapture data for the Kootenai River White Sturgeon was used for this analysis. The dataset required some initial “cleaning” with respect to assigning age-at-release to some fish, updating capture histories, and reconciling minor data entry errors. Thus, the final sample for use with these analyses was slightly different from the 125,948 in Beamesderfer et al. (2013; Table 2).

Closure Assumption

The three-day sampling efforts in summer 2013 yielded 66 juvenile sturgeon captures at rkm 130 and 54 juvenile captures at rkm 141. Of these initial captures, there was a recapture at rkm 141 and no recaptures at rkm 130 within the three-day sampling period. The estimates of capture and recapture probability were not estimable (too few recaptures), and sturgeon abundance could not be estimated at either site. It was concluded that either the closure assumption was violated within the three-day sampling period (e.g., there was substantial fish movement within even this short time period), or capture and recapture probabilities were inherently low and would require more intensive sampling to estimate “well.” Based on these efforts, it is unlikely that a robust design sampling approach would be worthwhile for estimating White Sturgeon abundance in this system.

Annual Survival

The analyses of annual survival of White Sturgeon incorporated capture and recapture information from 122,642 fish. M-array summaries of the input and recapture data for each of the four groups used in the analysis can be found in Table 2.

The comparison to the seven models in Beamesderfer et al. (2013) revealed that both approaches selected the more parameterized models that included age effects (Table 3). In the current analysis, all weight was in a single model, and it was clear that there were age-specific patterns in annual survival. Patterns in annual survival were generally similar for each analysis, except that this analysis incorporated true age effects that were not confounded with time-since-release.

After this initial model set was considered, the analysis was expanded to include other sources of variation in annual survival, including linear and quadratic trends across years and various combinations of individual covariate effects. In total, 45 models were considered in the analyses of patterns of annual survival (Table 4). The best model to explain variation in White Sturgeon survival was one that included annual variation in age-1 survival with the additive effects of fork length and release season, annual variation in age-2 survival, and constant survival in age-3+. Most closely ranked models also had annual variation in age-1 survival and constant age-3+ survival. Model selection favored a three-age-class structure over a two-age-class structure, and annual patterns in survival were best explained by year effects rather than trends across years.

Capture probability was also estimated as part of the survival analyses. Strong evidence of additive yearly variation and fork length in capture probability was found; no other models of capture probability were competitive. When year and fork length were modeled separately, it was clear that year was the stronger effect on capture probability of White Sturgeon. This additive year and fork length effect in capture probability was included in all top models. Models where capture probability was constant or a function of age class or a trend across years received no support. The strong yearly variation in capture probability closely mirrored that reported by Beamesderfer et al. (2013) with levels ranging from 0.11 to 0.23 between 1995 and 2001, but then dropping below 0.09 in all subsequent years (Figure 2).

The MCMC analysis improved estimates of survival and capture probability for some years and age classes. Because this approach reduced numerical convergence and estimation problems encountered with the CJS approach, these results were used to illustrate patterns in age-specific annual survival. For age-1 sturgeon, annual survival generally declined rapidly across the study period from 0.88 in 1992 to less than 0.13 after 2003 (Figure 3). The general pattern in yearly estimates was a close match to those reported in Beamesderfer et al. (2013). For age-2 fish, the pattern was less clear, although annual survival was generally much greater than for age-1 fish (Figure 4). The extremely low estimates in 2002 and 2004 (Figure 4) were due to a release effect on age-2 survival and are discussed at the end of the next section. Annual survival for age-3+ fish was best explained by a model without annual variation and the estimate was $\phi = 0.927$ (SE = 0.006).

Covariate Effects on Survival

The final model set included models that incorporated most of the individual covariates that were included in the dataset, except for release location (Table 4). Three of these covariates had strong effects on age-1 survival. The hatchery effect was negative ($\beta_{Hatchery} = -0.17$ [SE = 0.06]), which indicates that the survival of fish from the BC hatchery was greater than that of fish from the KTOI hatchery. This finding was similar to that of Beamesderfer et al. (2013). Both fork length ($\beta_{FL} = 0.11$ [SE = 0.01]) and weight ($\beta_{Weight} = 32.65$ [SE = 1.72]) had strong positive effects on age-1 survival, indicating that longer and heavier fish had greater survival to age-2 than did shorter or lighter fish. Additive and multiplicative models were also included in this analysis to account for other patterns in covariates, although multiplicative models were not well supported.

The influence of release season on annual survival was also explored in some detail. Using the best model (see Table 4) but fixing years constant because of computing time, the probability of a 25 cm age-1 sturgeon surviving to the next year was predicted as a function of its release season (spring, summer, fall, or winter). This prediction showed that spring release fish had the greatest estimated annual survival, and that annual survival steadily declined through summer, fall, and winter (Figure 5). The survival of winter-released fish to the following spring, despite the short time interval, was approximately 25% that of a spring-released fish.

After the initial analyses were completed, feedback from other researchers raised concerns about a possible confounding between hatchery origin and release season, and between fork length and release season. To address these concerns four models were added, two each with additive and multiplicative interactions of these effects added to the best model from the initial analyses. The results showed that models incorporating fork length were a significant improvement with the additive and multiplicative models, respectively, ranking as the top two models (Table 4). The multiplicative effect was estimated at -0.26 with a large standard error and a 95% confidence interval that included zero (95% CI was -0.64 to 0.12). This suggests that there was at least some seasonal balance in numbers of releases from both hatcheries, a conclusion that is at least partially affirmed by looking at the raw releases by season and hatchery (Table 5).

The predicted survival of age-1 fish varied as a function of release season with spring releases having significantly greater survival than fall releases (Figure 6). In general, annual survival was much greater from 1999 to 2002 and dropped considerably after 2005. Annual survival for spring releases only was also evaluated, and it was found that larger fish had significantly greater survival than small fish in most years, although some of the estimates for 30 cm fish were estimated imprecisely (Figure 7). However, in no year did the 20 cm fish have a greater annual survival rate than any of the larger fish. The survival difference between a 20 cm fish and a 30 cm fish was striking in some years, but in other years there were no differences. For some years (1999-2002) the difference between a 25 cm fish and a 30 cm fish was less obvious, and mainly arose because many of the 95% confidence intervals on estimates for 30 cm fish were large. But for at least a couple of recent years (e.g., 2008 and 2010), this was not the case and 30 cm age-1 fish were predicted to survive at much greater rates than 25 cm age-1 fish in those years. The underlying pattern was probably more complex; however, it is likely that a 30 cm age-1 fish had a greater chance of surviving to age-2 than a 20 or 25 cm fish.

Finally, a model where age-2 survival differed between newly-released fish and those that survived from age-1 was developed by modifying the top model from the initial survival analyses. This new model outperformed the previous best model by almost 108 ∆AIC units and showed that the survival of newly-released age-2 sturgeon was significantly lower than those released at age-1. The predicted annual survival of newly- and previously-released age-2 sturgeon, respectively, was 0.067 and 0.935 (2001), 0.047 and 0.642 (2002), and 0.033 and 0.959 (2004). These differences are more than ten-fold across all three years and show that newly-released age-2 fish have much lower annual survival than fish that grew to age-2 in the river.

Virtual Population Analysis

This analysis provided estimates of the number of fish by release year that comprised the total population during each year of the study period (Figure 8). The estimated population size was small through 1997, never having more than 200 fish. From the late 1990s to the early 2000s the population was estimated to grow rapidly to nearly 8,000 fish by 2004. The population more than doubled in 2005, but in subsequent years it ranged from an estimated 12,000 to 15,000 fish. This differed slightly from the results of Beamesderfer et al. (2013), which showed similar growth through 2004, but then showed that the population peaked later (in 2007 instead of 2005) and had lower estimates of the population size since about 2001.

DISCUSSION

The findings from the analyses reported herein add to an expanding knowledge of the demography of the Kootenai River White Sturgeon. More importantly, they provide additional insight into survival patterns of this species, some of which may help shape future management of this population. The most important findings are as follows:

1. These analyses provide the first age-specific estimates of annual survival for the Kootenai River White Sturgeon; previous analyses of these data have addressed components of survival and time-since-release (Justice et al. 2009, Beamesderfer et al. 2013). As in many long-lived vertebrates, survival in early life stages is often low and difficult to estimate. Estimates of age-1 survival have declined dramatically since the early 1990s. Annual survival of age-2 and older fish has been much greater and is showing no evidence of a decline. Understanding why age-1 survival has declined so sharply should thus be a priority for future study.
2. Estimates of capture probability were similar to those from earlier analyses of these data, confirming the slow decline in this parameter through time. The similarity to results from Beamesderfer et al. (2013) is not surprising because both analyses included year effects on capture probability. This pattern of decline has likely resulted from increases in sturgeon density or possibly other factors..
3. Survival analyses confirmed the importance of fork length, weight, and hatchery source as correlates with annual age-specific survival. Fork length and weight were positively correlated with age-1 survival and predicted that longer and heavier fish at release had a significantly greater chance of surviving to age-2. The clear message was that size at release should be kept as large as possible. The source of fish for stocking was also an

important predictor of age-1 survival, with fish reared in British Colombia having significantly greater survival than those reared in the KTOI hatchery.

4. The findings presented in this report represented true age effects rather than survival as a function of time-since-release. From an ecological perspective, an understanding of true age effects on survival represents the best approach to understanding patterns of annual survival. Differences between the survival estimates presented herein and those from a previous analysis (Beamesderfer et al. 2013) were most evident in age-2 fish. Although the datasets were similar for both analyses, and the population contained relatively few age-2 fish, the differences in modeling true age as opposed to time-since-release can still result in substantially different estimates of annual survival. This was ultimately a methods issue at the analysis stage, and in the future it is suggest that only true age effects be included in models of annual survival.
5. Analyses of the influence of release season showed that this was an important predictor of annual survival with spring > summer > fall > winter. Justice et al. (2009) discussed the influence of size and stocking density on release strategies, and the present study built on their approach. Annual survival of spring released sturgeon was 40% greater than survival of fish released in summer. Based on these results, limiting future releases to spring would likely result in significantly greater survival to age-1 and should be a priority if maximizing annual survival is a recovery goal.
6. The virtual population analysis repeated here was similar to that of Beamesderfer et al. (2013) except that it peaked earlier (in 2005 versus 2007) and indicated the overall population was slightly larger. These differences probably resulted from the influence of true age effects in survival, especially since 1999 when larger numbers of age-1 fish were released.
7. Two three-day sampling periods, during which the goal was to estimate capture and recapture probabilities under the assumption of population closure, were unsuccessful

because sufficient recaptures could not be achieved. Thus, continuing this sampling scheme to use a robust design to estimate population size is not recommended.

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TABLES

Table 1. Releases of White Sturgeon by year and age class in the Kootenai River system from 1992-2012. Not shown are 2,116 unknown-age fish that were included in the dataset, but not subsequently incorporated into any survival analyses. A total of 122,642 juveniles were included the analyses.

Year	**age-1**	**age-2**	**age-3+**
1992	105	13	
1993			
1994		123	
1995			
1996			
1997		1959	77
1998			42
1999	309		10
2000	2187	1	4
2001	3943	2081	4
2002	7140	4172	7
2003	11219		914
2004	12540	3001	21
2005	1242		8
2006	2368	33	31
2007	6801		2
2008	3053		
2009	14739		7
2010	14031		7
2011	15338		11
2012	12980		3
TOTAL	**107995**	**11383**	**1148**

Table 2. Summaries of input data in *m*-array format for White Sturgeon released into the Kootenai River system from 1992-2012. Shown are separate *m*-arrays for each of the four groups used in the analysis: a) group 1 (age-1 fish), b) group 2 (age-2 fish), c) group 3 (age-3+ fish), and d) group 4 (unknown-age fish). The number of fish that comprised each release [R(i)] is shown in rows by sampling occasion (Occ.), which corresponded to years (Occ. 1 is 1992, Occ. 2 is 1993, etc.). The j columns (2 through 21) show the number of fish first recaptured on that occasion; the total number of recaptures is shown in the rightmost column.

(a) Age-1 fish

		j =																				
Occ.	R(i)	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	**Total**
1992	105	1	0	14	21	4	3	8	2	0	2	2	3	0	0	0	0	0	0	0	0	**60**
1993	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1994	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1995	14				3	1	3	1	3	1	0	0	0	0	0	0	0	0	0	0	0	**12**
1996	24					4	1	3	3	0	0	1	0	0	0	0	0	0	0	0	0	**12**
1997	9						1	3	0	0	2	0	0	0	1	0	0	0	0	0	0	**7**
1998	8							1	0	1	1	0	1	0	0	0	0	0	0	0	0	**4**
1999	325								8	15	7	4	2	3	1	3	3	5	2	1	4	**58**
2000	2203									141	54	51	51	44	30	26	23	9	22	10	10	**471**
2001	4101										54	63	52	22	25	35	41	31	13	14	19	**369**
2002	7260											32	11	18	17	9	22	12	6	7	9	**143**
2003	11372												8	2	12	4	16	15	6	13	12	**88**
2004	12668													75	83	83	123	96	94	86	57	**697**
2005	1406														17	14	18	8	4	9	6	**76**
2006	2554															15	31	18	15	26	11	**116**
2007	6990																24	23	22	24	10	**103**
2008	3354																	59	45	54	36	**194**
2009	15015																		118	91	45	**254**
2010	14378																			76	43	**119**
2011	15749																				57	**57**

(b) Age-2 fish

Occ.	R(i)	j = 1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	**Total**
1992	13	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	**3**
1993	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1994	123			12	11	9	5	3	5	1	7	0	2	0	1	0	0	0	0	1	2	**59**
1995	12				5	2	2	0	0	1	0	0	0	0	0	0	0	0	1	0	0	**11**
1996	18					1	1	2	2	2	0	1	0	0	2	0	1	0	0	0	0	**12**
1997	1971						168	99	98	77	45	21	42	19	10	12	15	12	11	7	10	**646**
1998	176							11	23	9	9	1	4	1	2	2	1	3	0	2	3	**71**
1999	116								19	19	8	1	0	1	0	0	1	2	3	0	0	**54**
2000	148									33	13	4	8	3	2	3	1	1	3	0	1	**72**
2001	2223										116	56	69	40	58	41	65	47	20	23	20	**555**
2002	4370											11	23	8	22	3	14	14	6	4	11	**116**
2003	95												3	5	1	1	3	4	0	1	1	**19**
2004	3152													8	8	6	3	5	5	4	8	**47**
2005	85														2	5	1	4	0	1	1	**14**
2006	141															6	12	8	3	6	3	**38**
2007	79																9	6	0	6	3	**24**
2008	126																	10	2	10	4	**26**
2009	116																		9	10	4	**23**
2010	63																			5	5	**10**
2011	80																				5	**5**

(c) Age-3+ fish

		j =																				
Occ.	R(i)	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	**Total**
1992	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1993	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1994	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1995	0				0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1996	0					0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1997	77						58	19	0	0	0	0	0	0	0	0	0	0	0	0	0	**77**
1998	100							7	15	11	3	1	0	1	0	2	3	1	1	0	0	**45**
1999	36								5	1	2	1	1	0	0	0	0	0	1	1	0	**12**
2000	24									4	3	1	0	1	0	0	1	0	0	0	0	**10**
2001	20										2	2	1	0	0	0	0	0	0	0	0	**5**
2002	17											1	2	0	0	0	1	0	0	0	0	**4**
2003	920												29	10	14	16	23	12	7	13	10	**134**
2004	54													1	1	1	1	0	1	1	2	**8**
2005	21														0	0	1	0	0	0	1	**2**
2006	46															1	3	3	4	3	2	**16**
2007	22																1	2	0	0	0	**3**
2008	34																	1	2	0	0	**3**
2009	26																		0	1	1	**2**
2010	23																			0	1	**1**
2011	30																				2	**2**

(d) Age unknown fish

		j =																				
Occ.	R(i)	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	**Total**
1992	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1993	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1994	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1995	1				0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1996	0					0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1997	0						0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1998	0							0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
1999	2								0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
2000	0									0	0	0	0	0	0	0	0	0	0	0	0	**0**
2001	2										0	0	0	0	0	0	0	0	0	0	0	**0**
2002	10											1	0	0	0	0	0	0	0	0	1	**2**
2003	13												0	0	1	0	0	0	0	0	0	**1**
2004	26													0	0	0	0	1	0	0	0	**1**
2005	11														0	1	1	1	1	1	0	**5**
2006	39															0	1	0	0	1	0	**2**
2007	264																13	11	8	5	3	**40**
2008	409																	19	22	27	13	**81**
2009	415																		18	20	13	**51**
2010	344																			22	21	**43**
2011	493																				16	**16**

Table 3 Comparison of seven models between the current analysis and those of Beamesderfer et al. (2013; Table 1). Models are ranked from best supported at the top to lowest supported at the bottom. Also shown are the number of parameters (K) and the model weight. This analysis was done as a comparison with the findings of Beamesderfer et al. (2013), only; it did not include any covariates, and the results were not used to make any inferences about sturgeon survival.

Beamesderfer et al. (2013)			Current analysis		
Model	K	Weight	Model	K	Weight
7	69	0.710	6/7	47	1.000
3	37	0.107	4	44	0.000
6	52	0.106	5	33	0.000
5	38	0.056	3	33	0.000
4	54	0.021	2	21	0.000
2	21	0.000	1	34	0.000
1	38	0.000			

Table 4. Model selection results for analysis of the annual survival of Kootenai River White Sturgeon from 1992-2012. The two parameters are annual apparent survival (Phi) and conditional capture probability (p). Panel (a) shows the fitting of the best model of capture probability to a simple age class model for apparent survival. Panel (b) shows only models with a ΔQAICc value <100; the effect on capture probability was an additive combination of year and fork length. Model effects include age class (a1 = age-1, a2 = age-2, a3 = age-3+), year (Year), fork length at release (FL), weight at release (Weight), hatchery, release season (R_season), patterns across the 21-year study that were constant (.), and linear (T) or quadratic (TT). Models could include effects that were either additive (+) or multiplicative (*). Models were ranked by ΔQAICc, and the model weight (all sum to 1) and number of parameters (K) are also shown.

(a) Capture Probability

Model	**ΔQAICc**	**Weight**	**K**
Year+FL	0	1.0	22
Year	242.27	0	21
Quadratic time trend (TT)	739.73	0	5
Linear time trend (T)	977.82	0	4
a1*Year, all others constant	1393.27	0	23
FL	1468.83	0	6
R_Season	1489.91	0	6
age class	1690.99	0	8
age-1 different	1704.50	0	5
Weight	1716.62	0	6
No effects	1723.84	0	5
Hatchery	1791.05	0	4

(b) Annual Survival

Model	**ΔQAICc**	**Weight**	**K**
age class: a1*year+R_Season+FL, a2*year, all others constant	0.00	0.73	42
age class: a1*year+R_Season*FL, a2*year, all others constant	2.00	0.27	43
age class: a1*year+R_Season+Hatchery, a2*year, all others constant	48.22	0	41
age class: a1*year+R_Season*Hatchery, a2*year, all others constant		0	

Table 5. Summary of releases of age-1 White Sturgeon by release season and hatchery in the Kootenai River system from 1992-2012.

Release season	Kootenai Tribe	British Columbia
Spring	1	56,741
Summer	105	0
Fall	30,582	7,500
Winter	12,960	0

FIGURES

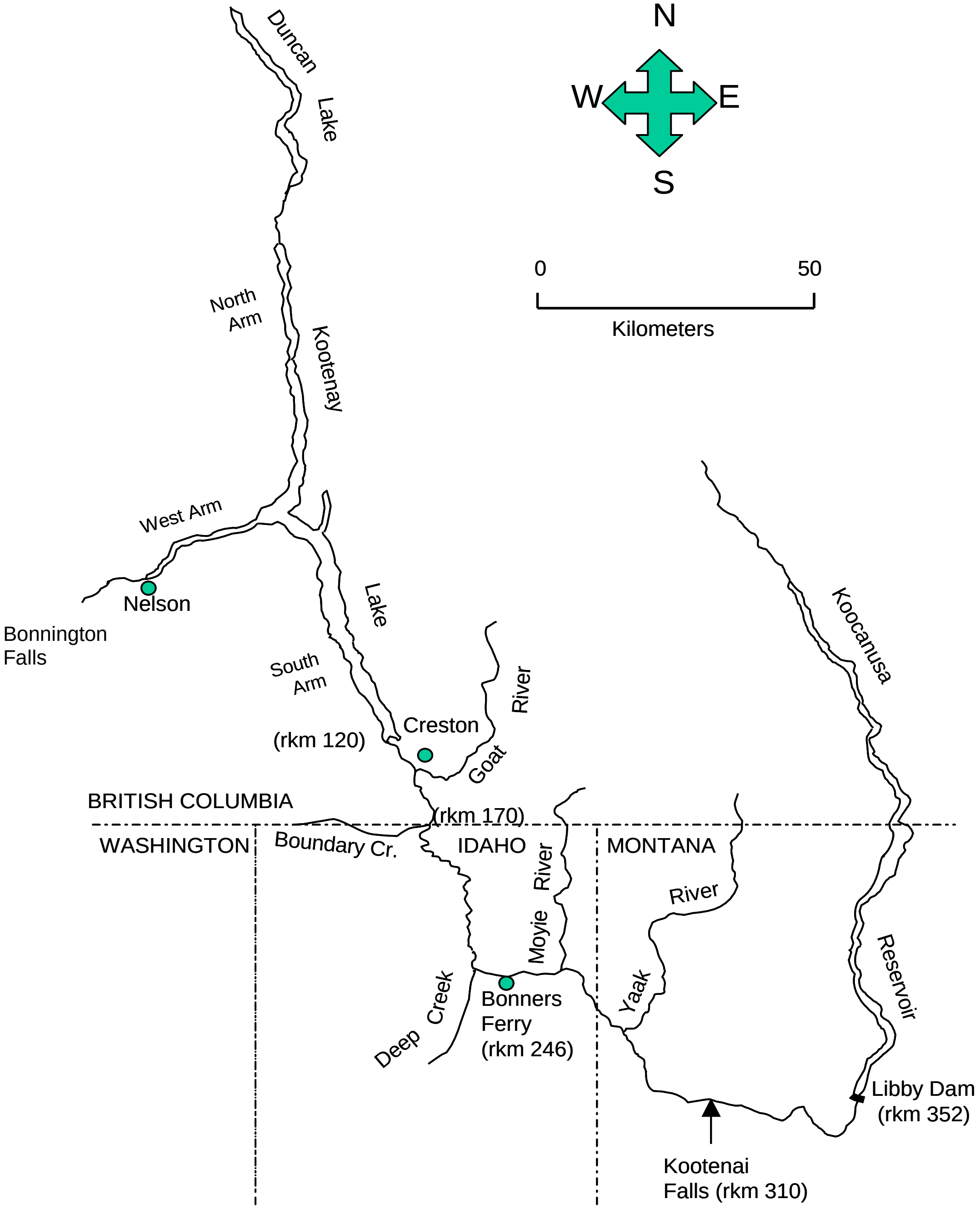

Figure 1. Location of the Kootenai River, Kootenay Lake, Lake Koocanusa, and major tributaries. The river distances from the northernmost reach of Kootenay Lake are in river kilometers (rkm) and are indicated at important access points.

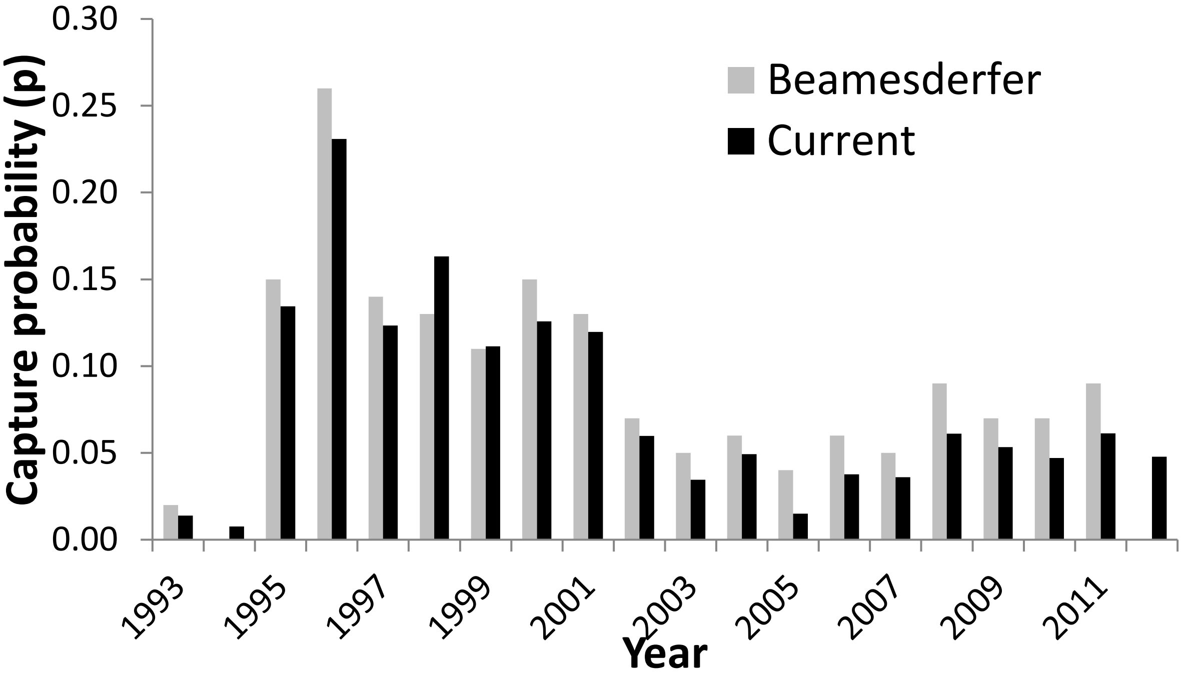

Figure 2. Estimated conditional capture probability of age-1 White Sturgeon in the Kootenai River system from 1992-2012. Capture probability estimates from the present study are shown along with those reported in Beamesderfer et al. (2013) for comparison. Estimates from both studies are missing from some years and indicate times when there were insufficient recaptures.

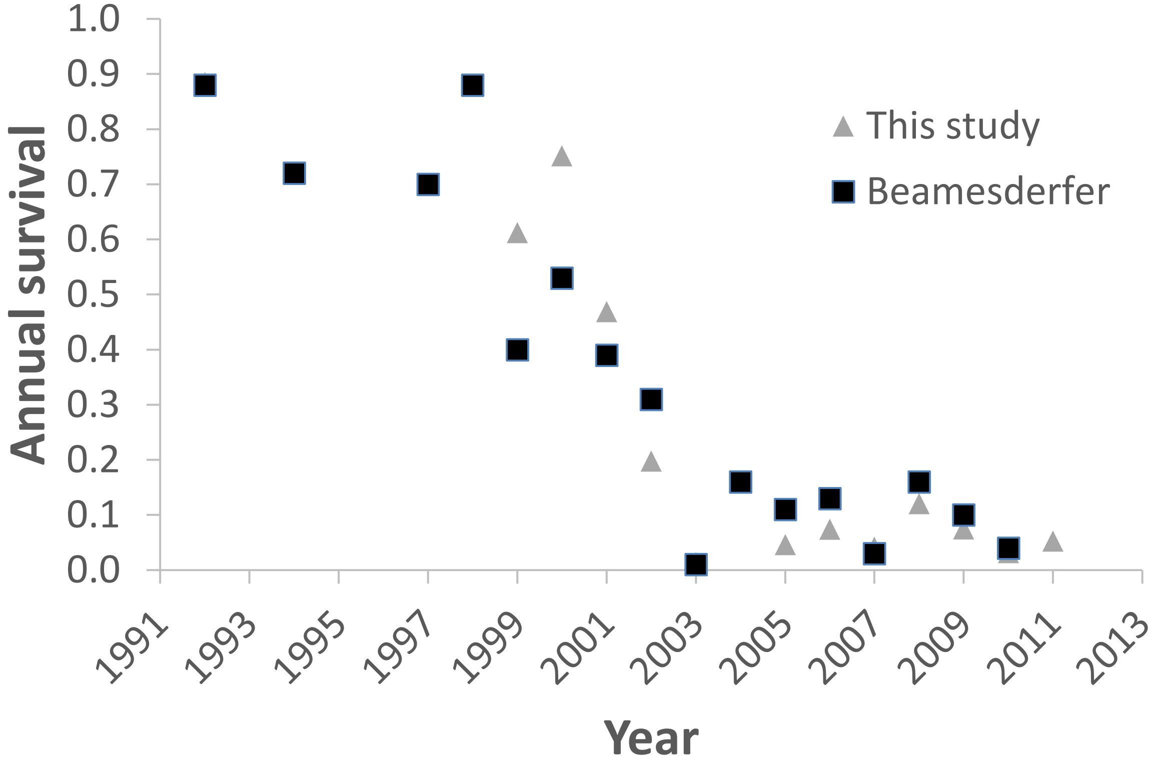

Figure 3. Estimated annual survival of age-1 White Sturgeon in the Kootenai River system from 1992-2012. Survival estimates from the present study are shown along with those reported in Beamesderfer et al. (2013) for comparison. Here, “Year” refers to the annual survival of a particular age class (this study) or release year (Beamesderfer et al. 2013). Estimates from both studies are missing from some years and indicate times when there were insufficient recaptures.

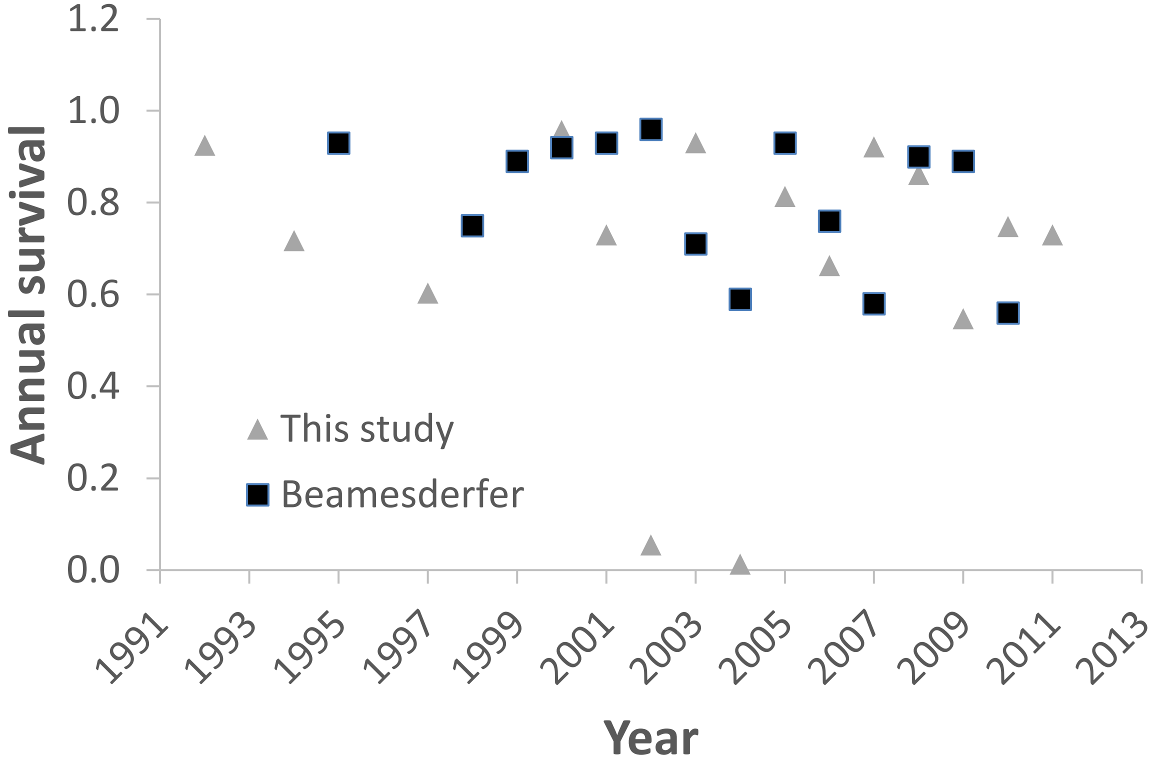

Figure 4. Estimated annual survival of age-2 White Sturgeon in the Kootenai River system from 1992-2012. Survival estimates from the present study are shown along with those reported in Beamesderfer et al. (2013) for comparison. Here, "Year" refers to the annual survival of a particular age class (this study) or release year (Beamesderfer et al. 2013). Estimates from both studies are missing from some years and indicate times when there were insufficient recaptures.

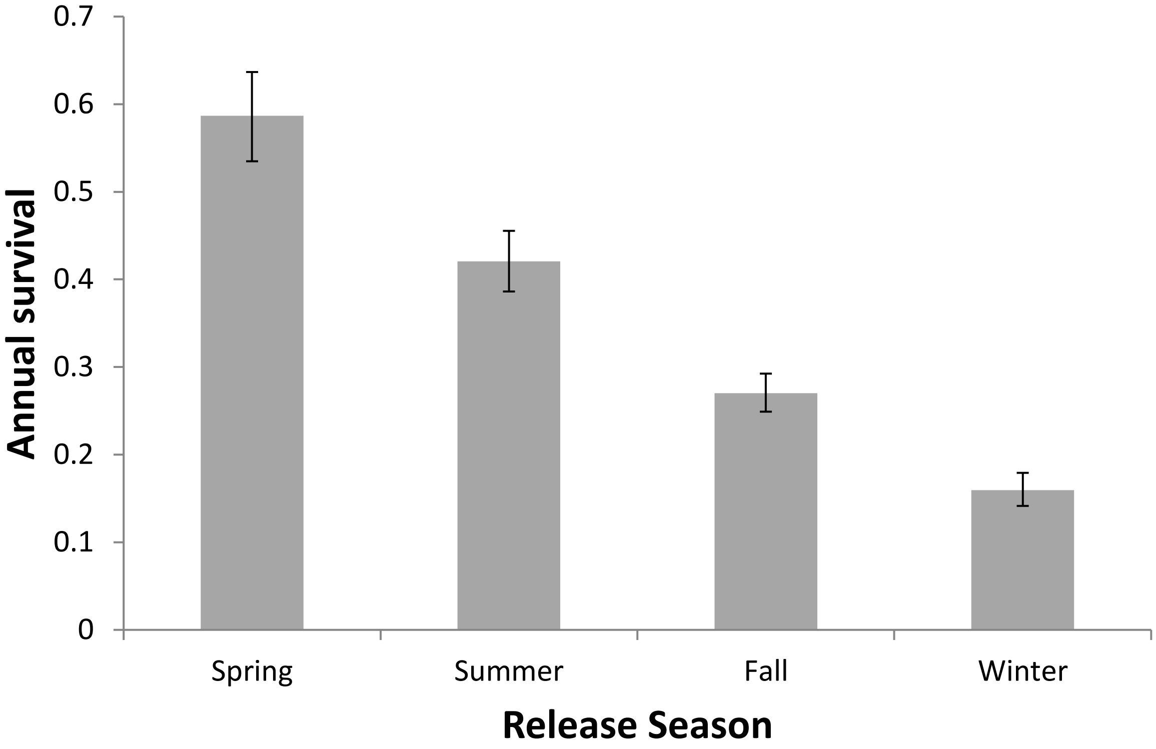

Figure 5. Predicted annual survival (and 95% confidence interval) of age-1 White Sturgeon in the Kootenai River system from 1992-2012. Using the best model from the survival analysis, annual survival was predicted with no annual variation for a juvenile sturgeon released in spring, summer, fall, and winter. Estimates do not account for potential confounding by hatchery source.

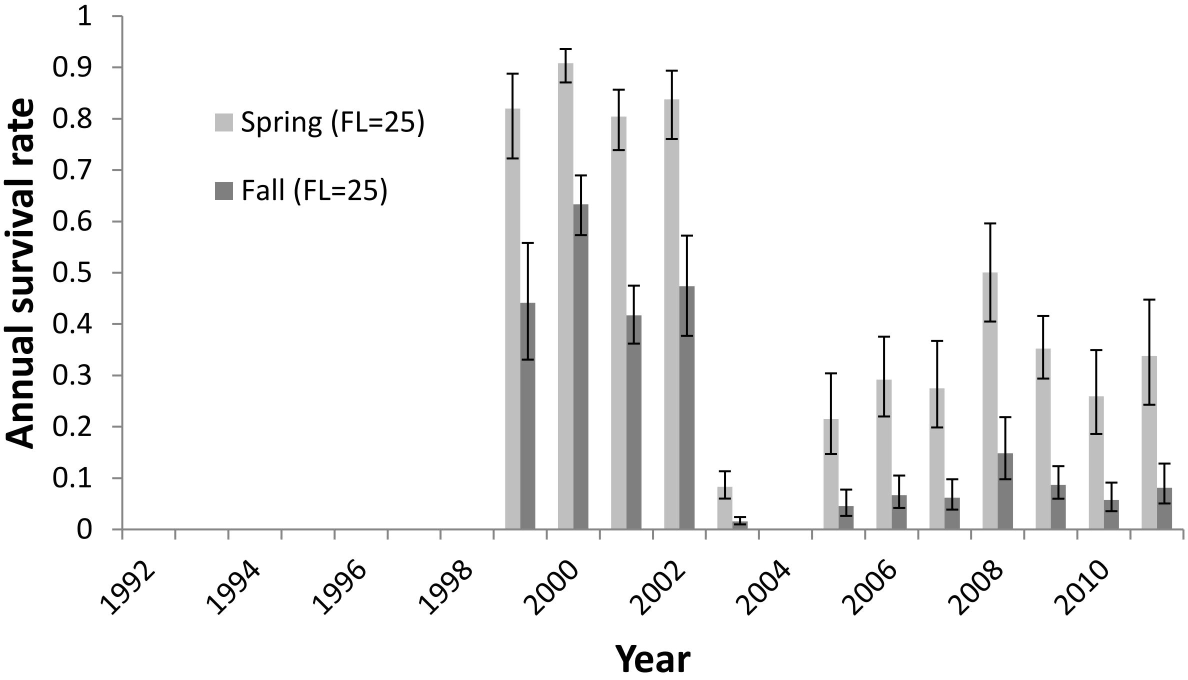

Figure 6. Predicted annual survival of age-1 White Sturgeon in the Kootenai River system from 1992-2012. Annual survival (and 95% confidence interval) is illustrated for fish that were released in the spring and fall. The years with no estimates are when age-1 fish were released. Estimates do not account for potential confounding by hatchery sources.

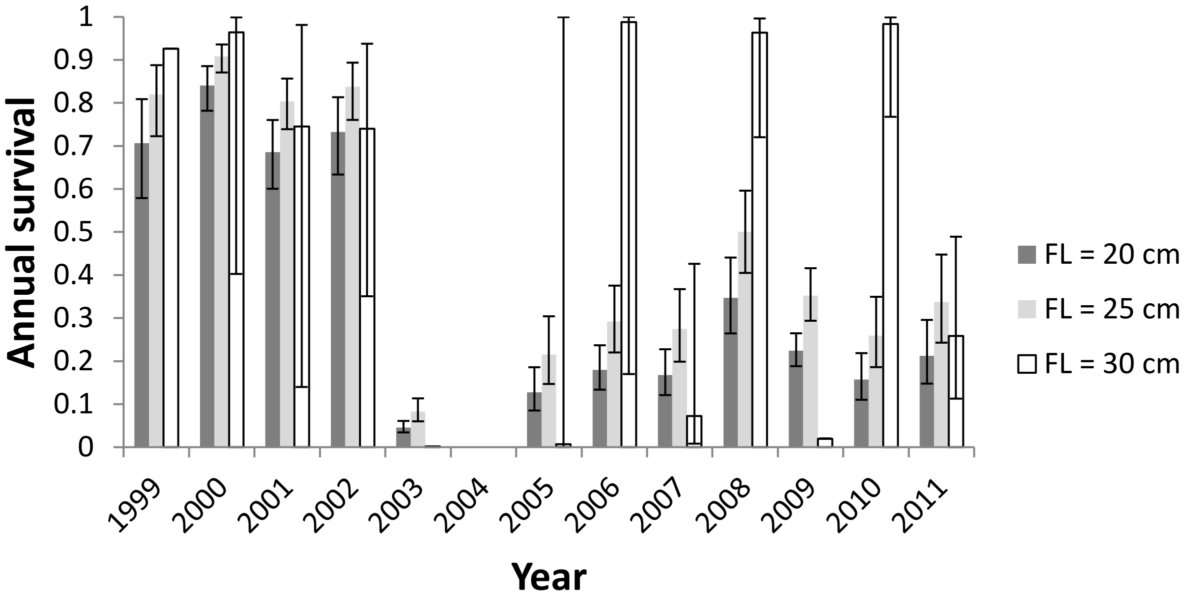

Figure 7. Predicted annual survival of age-1 White Sturgeon in the Kootenai River system from 1992-2012. Annual survival (and 95% CI) is illustrated for fish that were released at three different fork lengths (20 cm, 25 cm, and 30 cm) during spring only. The years with no estimates are when age-1 fish were released. Estimates do not account for potential confounding by hatchery source.

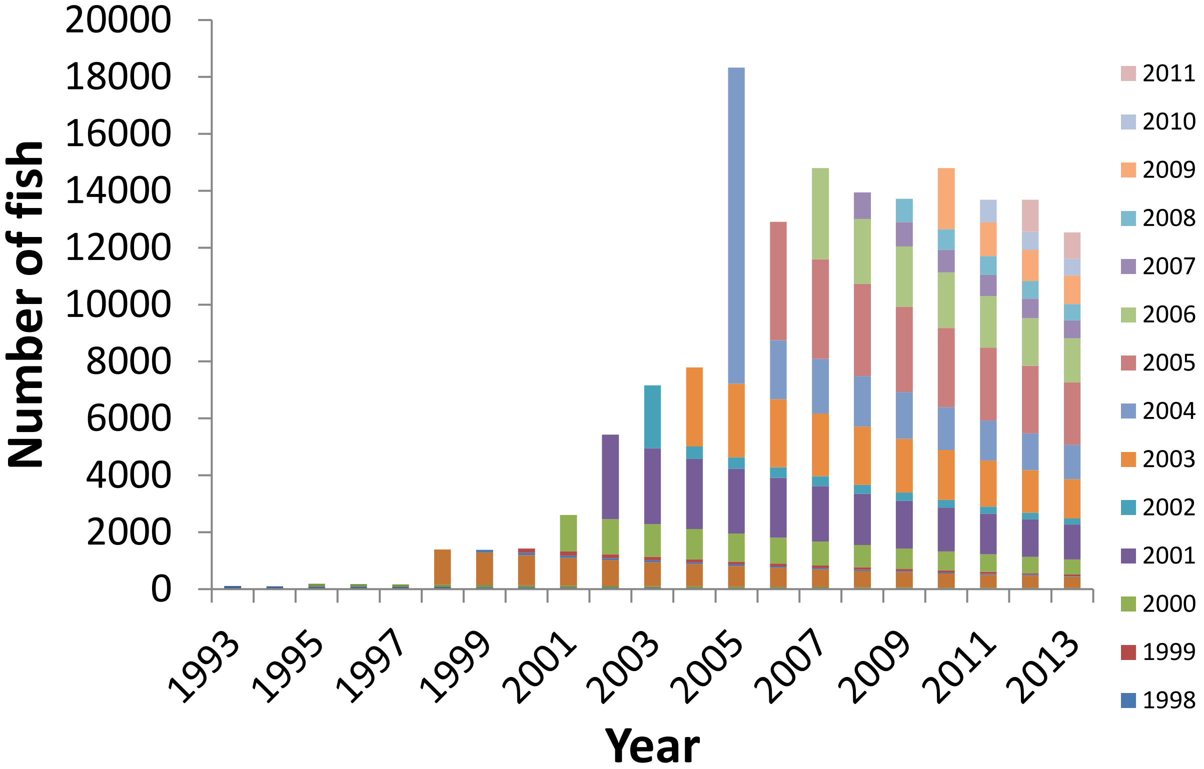

Figure 8. Estimated annual numbers of White Sturgeon of all age classes, by release year, for the Kootenai River system from 1992-2012.