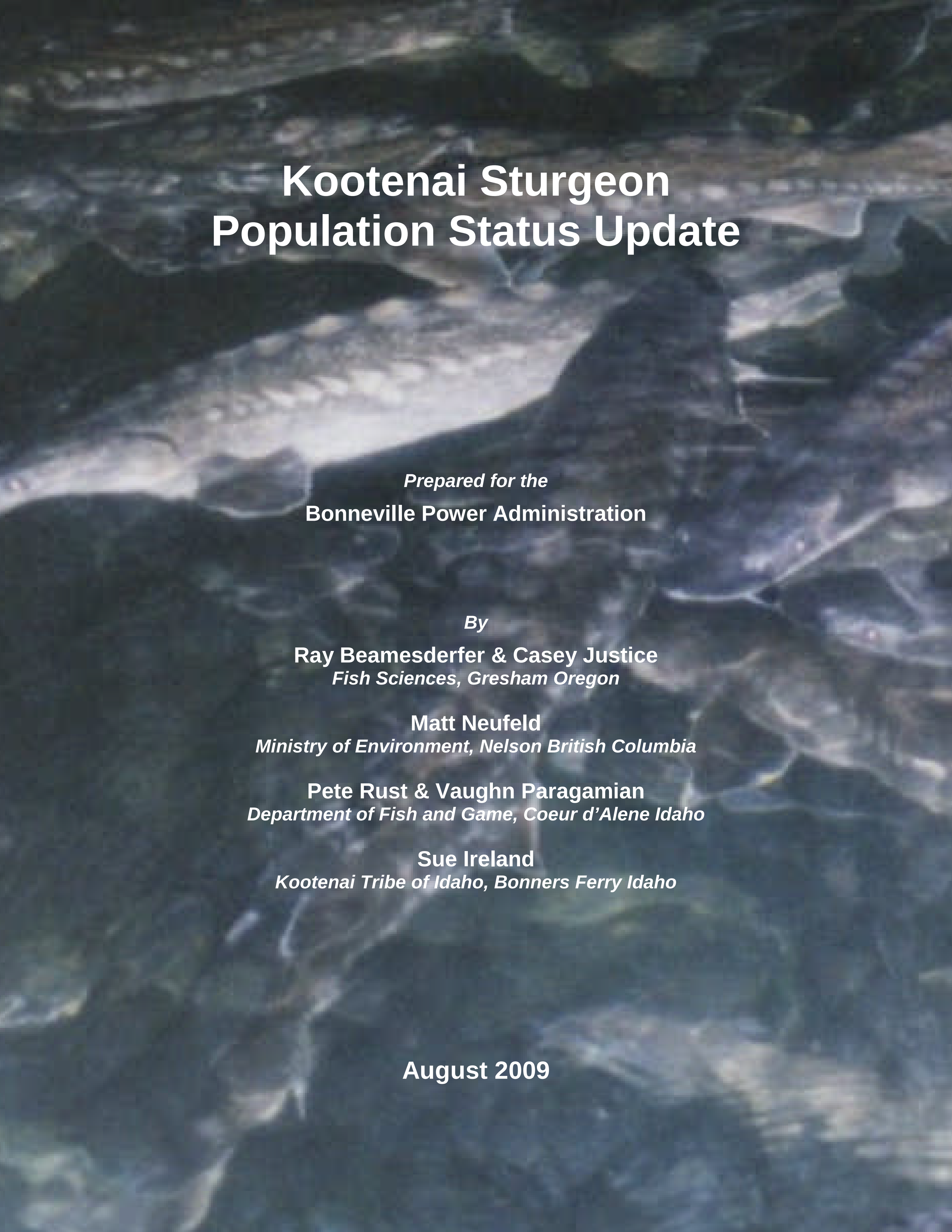

Kootenai Sturgeon Population Status Update

Prepared for the

Bonneville Power Administration

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August 2009

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Summary

1. This report provides an update on the status of the endangered wild population of Kootenai white sturgeon. A previous assessment analyzed mark-recapture data available through 2002 (Paragamian et al. 2005). This update incorporates new data collected through 2008.
2. Revised estimates of Kootenai sturgeon abundance suggest that the remaining population is larger than previously thought. Earlier estimates projected a 2007 population size at around 400 adults but revised estimates are for at least 1,000 sturgeon (95% confidence intervals = 800 – 1,400).
3. The rate of population decline also appears to less than previously estimated. Earlier analyses estimated a 9% annual rate of decline based on mark-recapture models and catch curve analysis. Current analyses estimate a 4% annual rate of decline based on updated mark-recapture analysis and telemetry data.
4. These results are consistent with observations of no declining trend in catch per unit effort and stabilization of adult recapture rates in hatchery broodstock collection efforts.
5. The differences between previous and current estimates results from violations of marked and unmarked fish mixing assumptions of the mark-recapture model used to estimate abundance and mortality. Marked:unmarked ratios were significantly less in fish captured from Kootenay Lake in samples from the Kootenai River. This pattern indicates that some fish dwelling in the lake are less likely to enter the river than others and some fish are resident in the river where they are captured more frequently.
6. It remains unclear whether the lake fish might represent slower or faster growing, younger or older, pre-reproductive or post-reproductive fish than are represented in the river-mixing component of the population. The size distribution of fish sampled in both areas is similar. Hence, neither the lake or river components of the population obviously appear to include a pool of smaller, younger fish that has not yet reached full sexual maturity.
7. Based on this information, the projected date when the remaining wild population would fall below 50 adult fish has been extended from 2030 to 2080. However, long range projections of this nature are highly uncertain due to uncertainty in population parameters.
8. In the near term encompassing the next 10-20 years, the revised population numbers appear to reduce concerns for the depth and duration of the interval of low spawner numbers as the wild population disappears before the hatchery fish begin to reach adulthood.
9. Results do not fundamentally change the long term outlook for this population or the strategy for recovery. Natural recruitment continues to fail, the population continues to decline, and extinction would be the inevitable outcome without implementation of effective recovery measures.
10. Qualified interpretation and precautionary application of this information continues to be appropriate for sturgeon recovery.

Introduction

This report provides an update on the status of the endangered wild population of Kootenai white sturgeon. The previous assessment included data available through 2002. This update incorporates new data collected through 2008 in continuing monitoring efforts by the Kootenai Tribe of Idaho, the British Columbia Ministry of Environment, and the Idaho Department of Fish and Game. This report includes are a summary of past assessments, a description of new information, and a discussion of implications to recovery activities. Details on methods and results may be found in the appendix.

Previous Assessments

Kootenai sturgeon status was last formally evaluated in 2005 based on an analysis of 25 years of mark-recapture data (Paragamian et al. 2005). That analysis synthesized sampling data of fish collected by set line, angling, and gillnet from 1977 through 2002. The dataset included 1,704 individually-tagged fish and 760 recaptures. Many fish were recaptured on multiple occasions and fish were at large up to 23 years between tagging and the latest recapture. This detailed and long term dataset allowed for the use of multiple mark-recapture statistical analysis using advanced maximum likelihood models.

The 2005 assessment estimated a decline in wild sturgeon abundance from approximately 9,000 in 1980 to just 800 fish by 2000 (Figure 1). Statistical confidence intervals on estimates where very wide during the earlier years but became progressively tighter in more recent estimates. The mark-recapture analysis also estimated an annual mortality rate of 9% per year.

The declining population trend was consistent with historical estimates of recruitment which indicated a near-total failure in the production of young sturgeon around 1960 (Figure 2). As a result of recruitment failure, the population now consists of an aging cohort of large, old fish. This trend is reflected in increases in average size and size distribution of the population over time (Figure 3).

Future trends in wild fish abundance were projected forward from the 2005 estimates based on the assumed annual mortality rate of 9% (Figure 4). Forward projections based on these rates estimate of just 400 sturgeon in 2007. At this rate of decline, the population is reduced by half every 7.4 years and fewer than 50 adult fish will remain by 2030 (Paragamian et al. 2005). Similar projections were made for the number of hatchery-produced fish reaching adulthood. Hatchery fish released beginning in 1990 can be expected to begin recruiting to the adult population after year 2020. The simulations estimated that relatively few adult sturgeon would be available for spawning between 2010 and 2025.

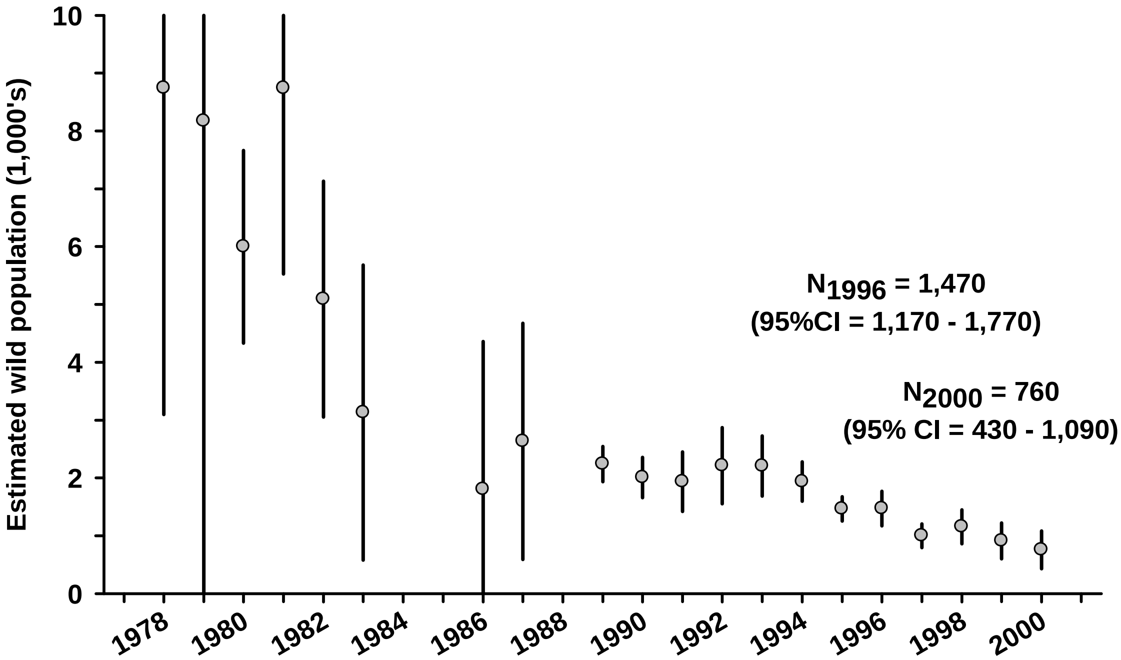

Figure 1. **Estimated abundance of wild white sturgeon in the Kootenai population, 1997-2001 (Paragamian et al. 2005).**

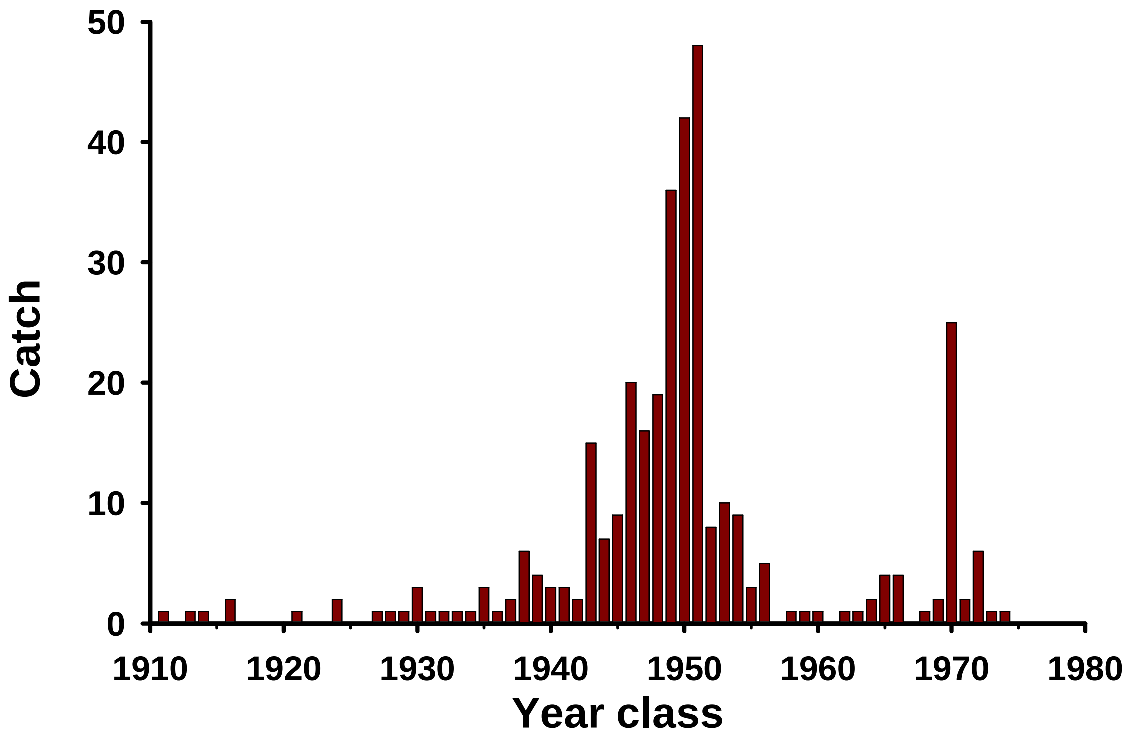

Figure 2. **Year-class frequency distribution of Kootenai River white sturgeon captured from 1977 to 1983 (Paragamian et al. 2005). Estimates are uncorrected for effects of mortality which are expected to reduce the frequency of older fish in the dataset but are corrected for aging errors estimated by Paragamian and Beamesderfer (2003).**

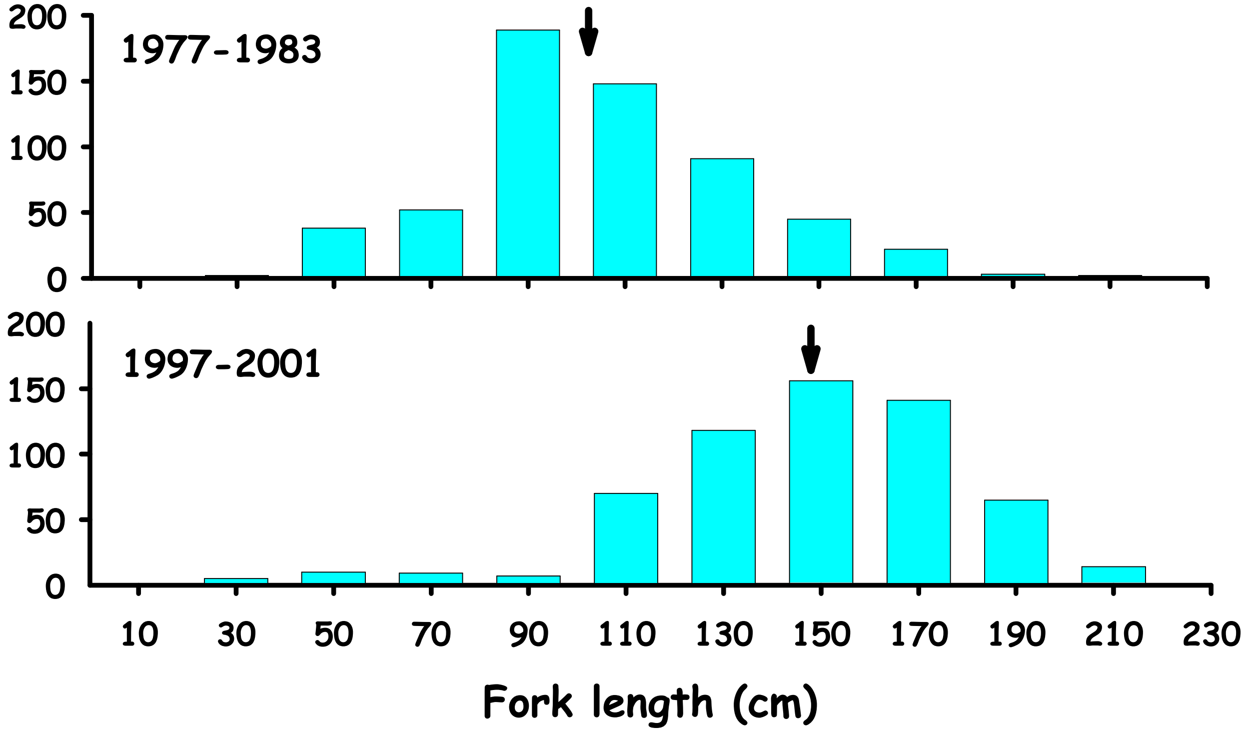

Figure 3. **Length-frequency data of Kootenai River white sturgeon during early and recent sample years (Paragamian et al. 2005).**

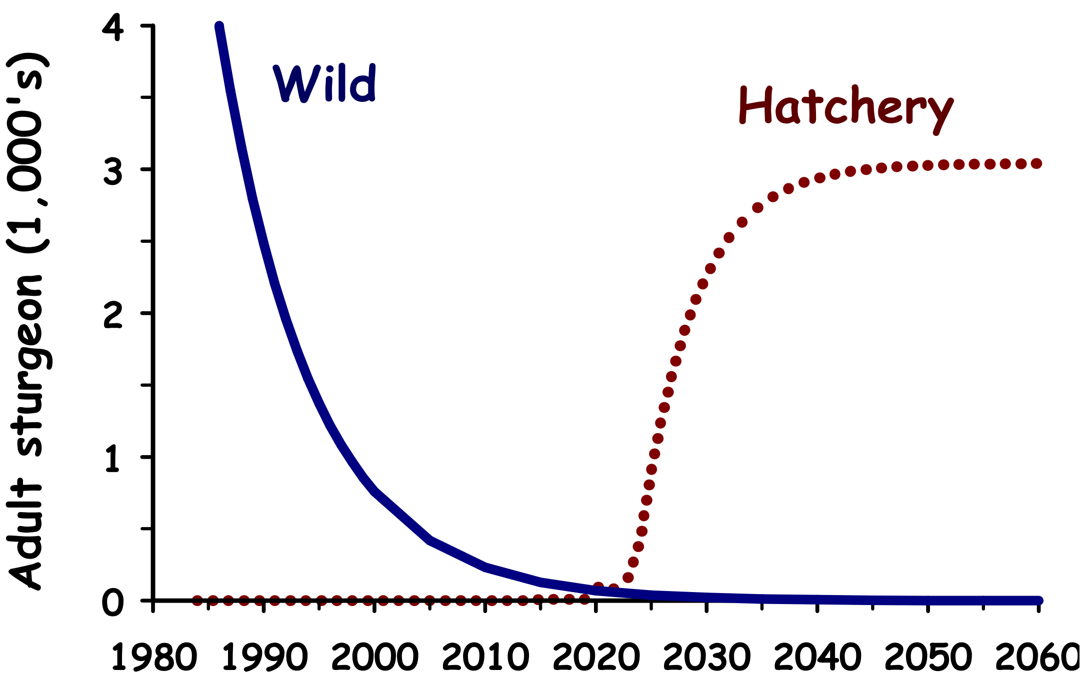

Figure 4. **Simulated population size for Kootenai River white sturgeon from 1980 to 2080 based on the 2005 population assessment and a simple population model presented in Paragamian et al. (2005).**

New Information

More recent data collected since 2002 provides a means of verifying and calibrating sturgeon population projections made in 2005. The recent dataset included 2,082 individually-tagged fish, 1,761 recaptures, and fish at large up to 30 years between tagging and the latest recapture. The number of recaptures in the dataset more than doubled as since 2002 as large numbers of fish from 30 years of release continue to be available for recapture (Table 4). The new information suggests that several projections of the 2005 analysis was overly-pessimistic although the essential findings were unchanged.

Catch rates of adult sturgeon have not continued to decline as projected from the 2005 simulations. Catch per unit effort should be a fair index of fish abundance if catchability (sampling efficiency) is relatively constant. Average annual catch rates are highly variable and not sensitive to small changes in abundance. However, large changes over an extended period of time should be apparent. Based on projections of declining abundance, we anticipated that it would become increasingly difficult to catch adults for hatchery broodstock in the near term. A decline in catch rates has not yet been observed (Figure 5).

The percentage of marked fish in the sample catch has also stabilized rather than continuing to increase as expected (Figure 6). In a closed population assuming no loss of marks, we would expect a progressively larger proportion of the fish captured to consist of marked fish as more unmarked fish are captured and marked each year.

New data also suggests that mortality estimates derived from the analysis (9%) overestimated the rate of decline of the wild population. Updated mark-recapture analyses estimated recent annual mortality rates averaging just 4% (including many of the same years included in previous estimates). Estimates were also derived from adult sturgeon tagged with transmitters in 2003-2006 and subsequently tracked through 2008 (see Appendix). Only 3 of 69 monitored fish appear to have died. Amortized for time at-large, telemetry numbers translate into an annual mortality rate of just 2% per year. If anything, the telemetry estimates might be expected to overestimate mortality if lost tags were counted as dead fish or the chances of fish dying increase due to capture and tagging. Fish selected for tagging do not also not represent the entire age/condition of fish covered by mark-recapture estimates. By selecting reproductive males and females, we may be missing some fish that are at higher risk of mortality (ie we may be tagging some of the most robust and healthy fish).

A key assumption of the mark-recapture analysis is that marked and unmarked fish in the population are equally vulnerable to sampling. In other words, the marked and unmarked fish must be randomly mixed. This assumption is rarely, if ever, met in the real world but mark-recapture methods can still provide reasonable estimates if the assumption is not grossly violated. The direction of any bias due to violation of this assumption is also known. Estimates of abundance are conservative where sampling is concentrated in a portion of the area and mixing is not random. The historical Kootenai sampling was concentrated in the river for adults during their spawning runs. This is where and when fish are most vulnerable to sampling and this sampling program also provides the fish needed for the conservation hatchery program. However, much of the population resides in Kootenay Lake for extended periods. As long as all the fish in the lake periodically cycled into the river where they were vulnerable to capture, tagging, and recapture, the corresponding mark-recapture estimates based on long-term sampling should have been fairly accurate. However, the new mark-recapture and telemetry data suggest a systematic bias in the assumptions of the mark-recapture model.

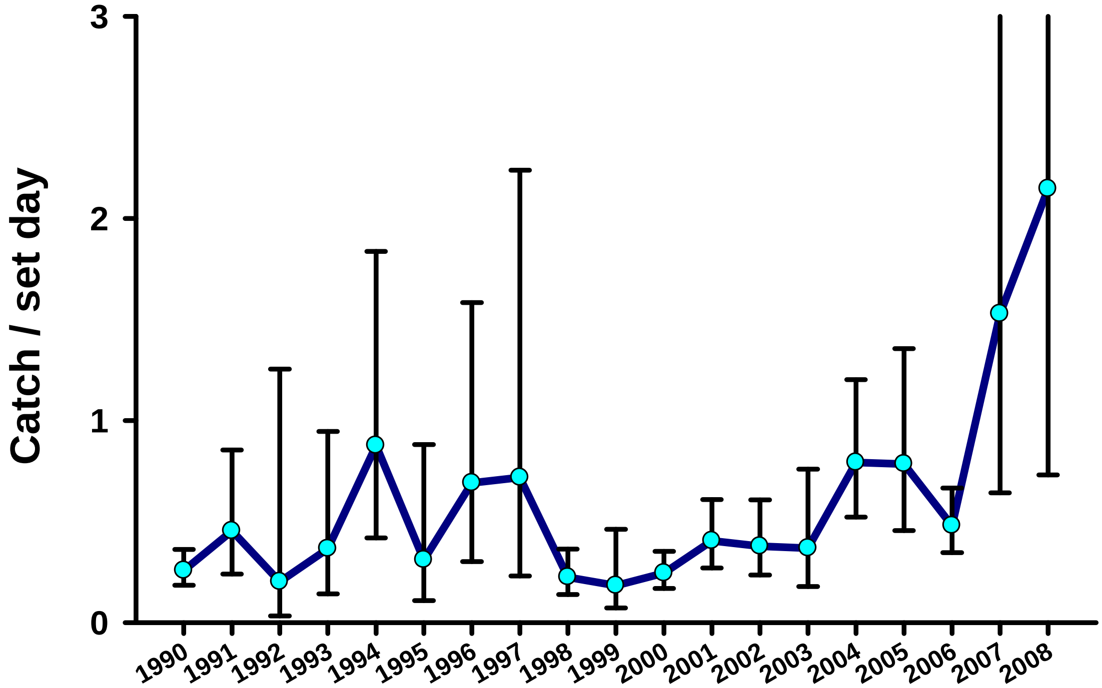

Figure 5. Sturgeon catch per angling day (24 hr of effort) from 2008 to 2008.

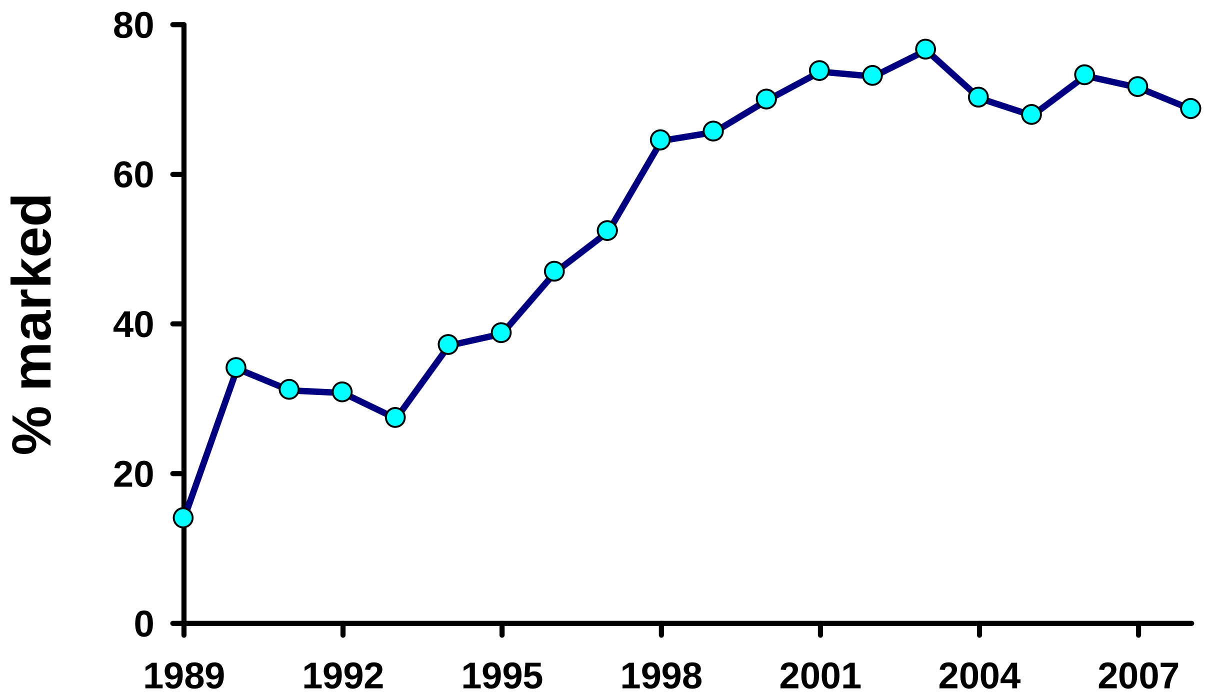

Figure 6. Percentage of the annul catch consisting of recaptures of previously tagged fish.

To test the accuracy of mixing assumptions, we compared marked-unmarked ratios of wild sturgeon from lake and river samples. Sampling effort in the lake has been relatively limited but pooled data from multiple years of sampling, primarily on the Kootenay River delta, provided a reasonable sample size for this analysis (Appendix Table 1). Lake samples consistently showed a lower mark rate than river samples (Figure 7) and the difference was statistically significant. These results confirm that the mixing assumption is violated and explain the discrepancies between observed and predicted trends in catch rates, recapture rates, and mortality estimates.

Figure 8 illustrates the effect of bias in estimates of abundance at different rates of tag mixing for a hypothetical fish population estimate of 500 fish. At 100% mixing of the population into sampled areas, the 500 fish estimate is the true abundance. Progressively lower rates of mixing of marked and unmarked fish result in a progressively greater underestimates of the actual abundance. For instance, a 50% mixing rate results in a 50% underestimate (500) of the actual abundance of 1,000. We estimated the equivalent of approximately a 50% mixing rate for Kootenai sturgeon based on differences in mark rates between Kootenay Lake and River samples. This hypothetical example illustrates the potential significance of a mixing bias for population estimates.

Revised analyses based on 1977-2008 data produced estimates of 1,000 naturally-produced Kootenai sturgeon in the population in 2007 (95% confidence intervals = 800 – 1,400). This estimate is substantially greater than the 400 fish projected based on the 2005 analysis which included data through 2002 (Figure 9). The difference results from the lack of nonrandom sampling of marked and unmarked sturgeon in the river and the lake.

Why some fish in the population are more or less likely to enter the river from the lake remains uncertain. The size distribution of fish sampled in both areas is similar (Figure 10). We initially suspected that the lake component of the population might include a pool of smaller, younger fish that had not reached full sexual maturity and did not have multiple years of participation in the spawning migration into the river. However, this was not apparent in the length-frequency distribution. Additional lake fish might also be post-reproductive or reflect sex differences in behavior. However, age and sex information is limited for lake samples. It remains unknown whether the lake fish might represent slower or faster growing, younger or older, pre-reproductive or post-reproductive, male or female fish than are represented in the river-mixing or river-resident components of the population.

The sturgeon population in the lake includes a mixture of fish that are more or less likely to enter areas of the river areas where they are vulnerable to sampling. The non-mixing component of the population is under-represented in the population estimates. The updated mark-recapture analysis essentially recalculates estimated abundance in previous years based on the new data which forces estimates from earlier years upward to match the current information. Over time, an increasing percentage of the non-mixing fish have the opportunity to be sampled which also gradually moves the estimates closer to the true abundance. However, mixing bias continues to result in underestimates of the population size.

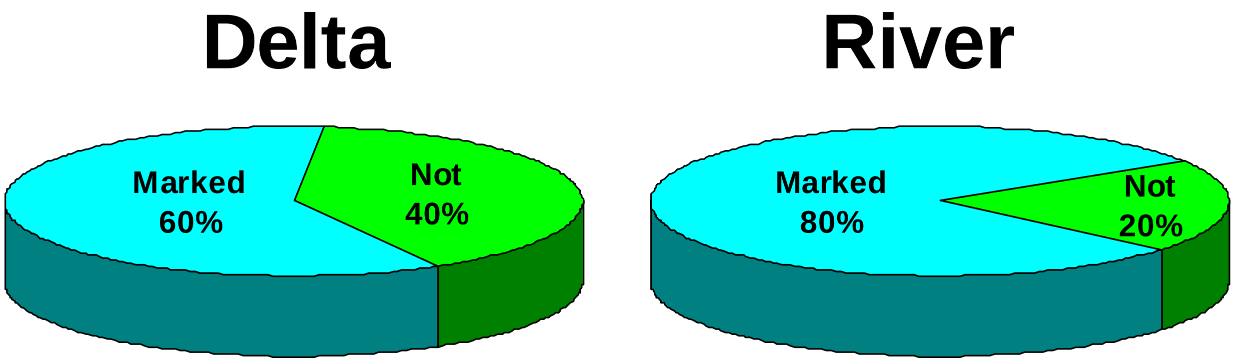

Figure 7. Marked fractions in sturgeon sampled from Kootenay lake and Kootenai River, 2000-2008.

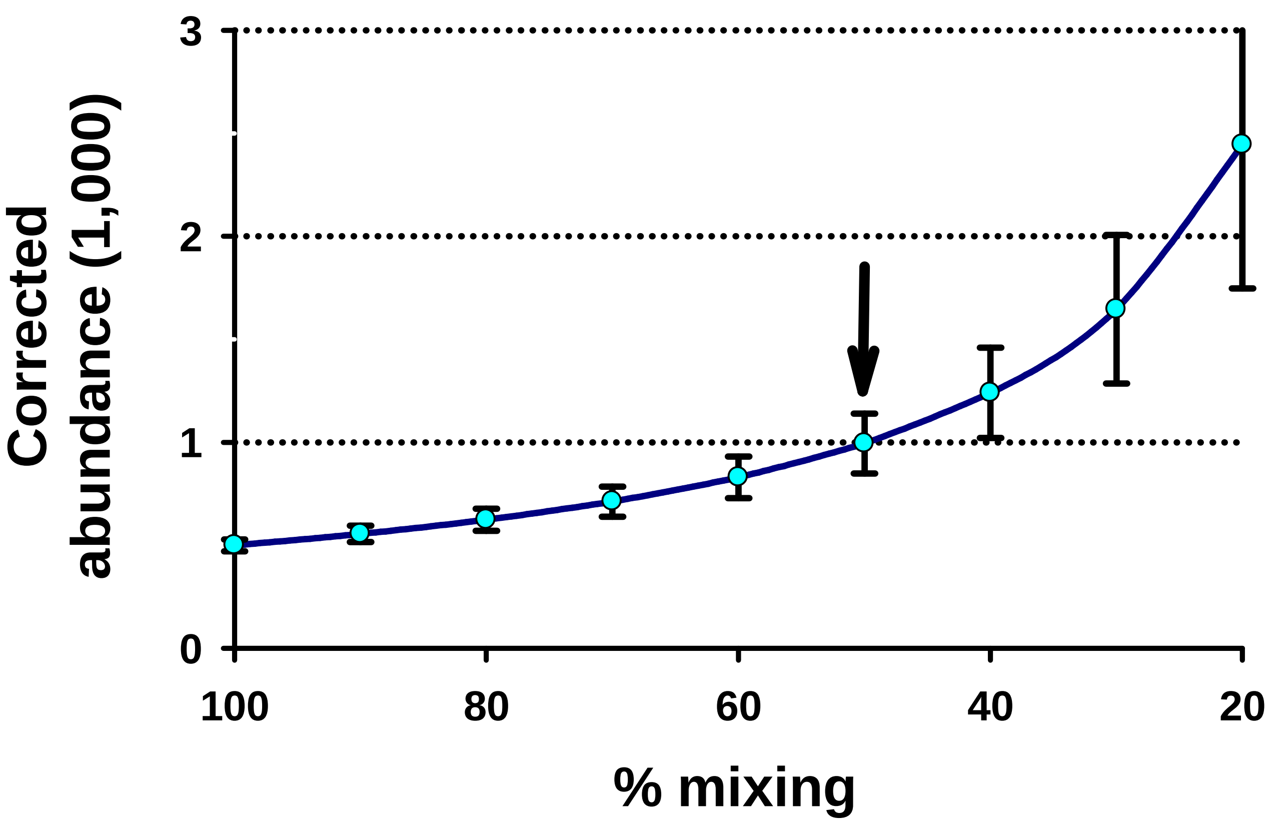

Figure 8. Relationship between abundance of a hypothetical population and the percentage of mixing between marked and unmarked fish in the catch. Error bars represent approximate 95% confidence intervals.

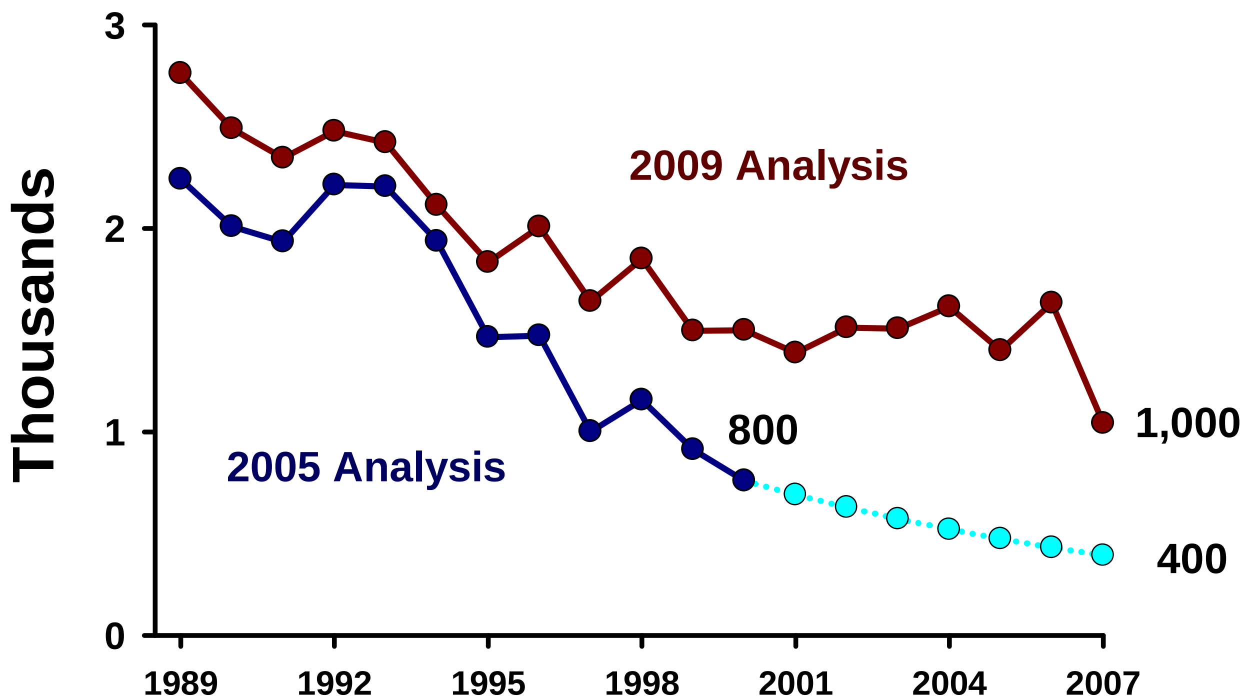

Figure 9. **Comparison of mark-recapture abundance estimates based on 1977-2002 data as reported in Paragamian et al. (2005) and updated analyses based on 1977-2008 data.**

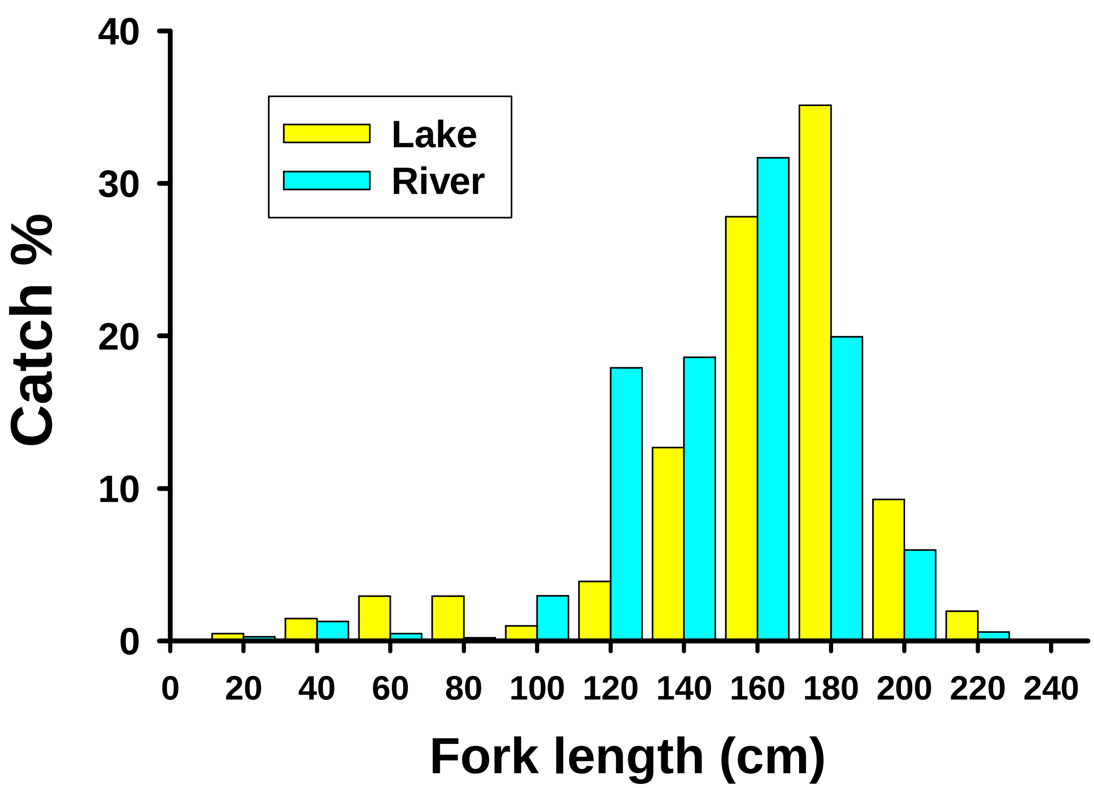

Figure 10. **Length-frequency distribution of sturgeon samples from Kootenay Lake and the Kootenai River.**

Implications

Revised estimates of Kootenai sturgeon abundance suggest that the remaining population is larger than previously thought. Earlier estimates placed the current population at around 400 adults but revised estimates are for at least 1,000 sturgeon. The rate of population decline also appears to less than previously estimated. Earlier analyses estimated a 9% annual rate of decline. Current analyses estimate a 4% annual rate of decline. Current estimates should be regarded as minimum numbers of the total population of naturally-produced fish. However, estimates might be representative of the effective spawning population in the Kootenai River.

The most significant implication of this finding is that the horizon for the decline and extinction of the remaining naturally-produced Kootenai white sturgeon population has been extended. Previous analyses projected the remaining wild population would fall below 50 adult fish by 2030 (Paragamian et al. 2005). Current analyses project that the remaining wild population will fall below 50 adult fish by 2080 (Figure 11). This change reflect the effects of both a greater current population size and a lesser annual mortality rate. Projections of the future population trajectory remain acutely sensitive to estimates of annual mortality. Long term projections of population trends based on this modeling approach should continue to be treated with extreme caution due to continuing uncertainties in sturgeon numbers. For instance, the model assumes that mortality rate remains relatively constant with increasing age and makes no allowances for the possibility of increased mortality or senility as the remaining wild individuals become very old. Model projections assume that fish from the existing population that were largely recruited prior to 1974 will be surviving to well over 100 yrs age. The maximum age and maximum reproductive age of white sturgeon is unknown but, but there is likely a maximum age above which fish mortality rates increase.

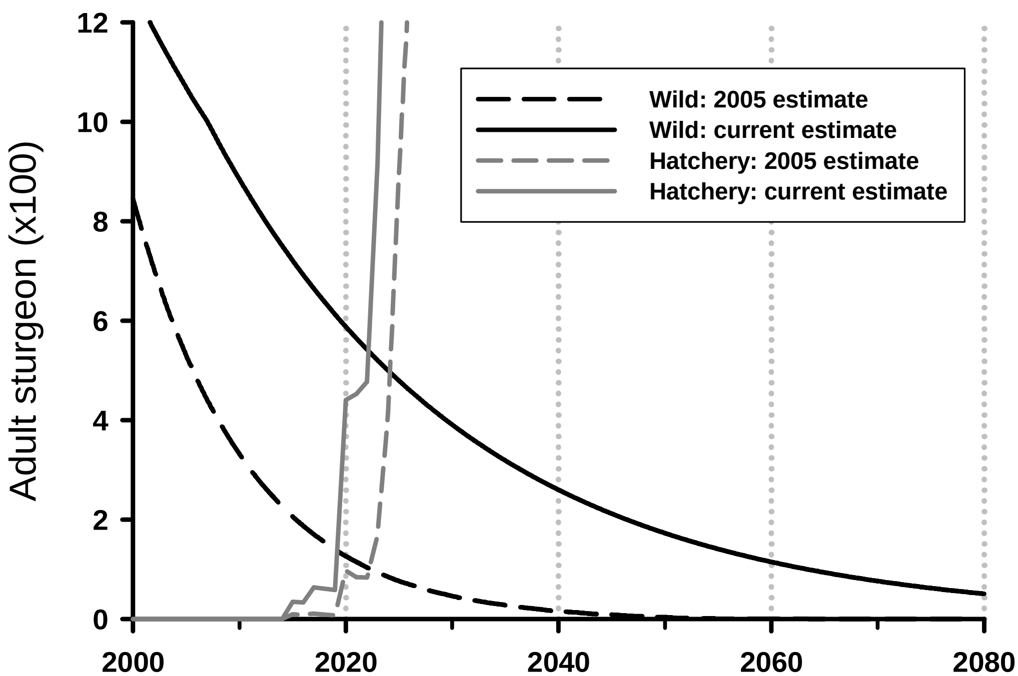

Figure 11. Model-projected estimates of wild and hatchery adult sturgeon population sizes based on 2005 and current analyses.

In the near term encompassing the next 10-20 years, the revised population numbers appear to reduce concerns for the depth and duration of the interval of low spawner numbers as the wild population disappears before the hatchery fish begin to reach adulthood. This increases the likelihood that adequate numbers of mature wild adults will continue to be available to support the conservation hatchery program in the foreseeable future. In this respect, the model projections are consistent with recent experience where the sampling crews have had little difficulty capturing hatchery broodstock. A significant wild population also remains to take advantage of any significant habitat improvements that may be implemented.

While the updated analysis appears to suggest that we have a little more time before the wild population fades than we previously feared, these results do not fundamentally change the long term outlook for this population or the strategy for recovery. Natural recruitment continues to fail and the population is still declining. Extinction would be the inevitable outcome without implementation of effective recovery measures. The conservation hatchery program continues to provide the only effective alternative identified to date for producing the next generation of Kootenai sturgeon. Effective large-scale habitat improvements continue to be needed to restore successful natural production.

Current estimates of the population size and trend in abundance represent the best available scientific information currently available but continue to be subject to significant uncertainty related to necessary assumptions of the analytical methods. More accurate estimates of sturgeon population status and dynamics would require increased sampling of the lake population. However, low catch rates in lake sampling mean that the necessary sampling effort would be large and costly. Results would likely not provide significant new information or substantially alter the direction of the recovery effort.

These estimates represent a series of progressive approximations that can be expected to continue to improve in accuracy and precision over time. The sensitivity of these estimates to additional years of data highlights the difficulty of making absolute population estimates for sturgeon where very small differences matter due to their long life span. In this case, the historical estimates proved to be conservative and population size appears better than was previously estimated. However, future analyses might just as easily produce new revelations that show current projections to be overly optimistic. Qualified interpretation and precautionary application of this information continues to be appropriate for sturgeon recovery.

Appendix – Analysis Methods & Results

Proportion of marked fish in river vs. lake

We summarized the total number of marked and unmarked wild white sturgeon captured in Kootenay Lake (i.e., <= rkm 132) and in Kootenai River from 1989 to 2008 to determine if the fraction of marked fish in the catch differed between lake and river sites (Table 1). Data was collected and provided by the Kootenai Tribe of Idaho (KTOI), Idaho Department of Fish and Game (IDFG), and the British Columbia Ministry of Environment (BC MoE). We excluded data from years prior to 1989 because the monitoring program during this period was largely experimental and sampling effort was sporadic.

The proportion of marked fish in the catch, an index of capture probability, was lower on average for fish sampled in the lake (mean = 36.8%) compared with fish sampled in the river (mean = 54.3%; Table 1). In river sites, the fraction of the catch that was marked increased steadily over time from about 15% in 1989 to about 70% in 2008 (Figure 12). The temporal trend in the marked fraction for lake sites was less clear due to low sample size, but a general increasing trend in recent years was apparent.

To determine if there was a statistically significant difference in the marked fraction between lake and river sites, we began by pooling the data into two groups including early years (1989-1997) and recent years (1998-2008). These groups were chosen to include years with relatively stable proportions of marked fish. We used two different statistical procedures to test for differences between lake and river sites including logistic regression, and chi-square analysis.

Logistic regression is a form of generalized linear model that is applicable to binomial data (McCullach and Nelder 1989; Dobson 2002). In this case, the binomial probability of interest is the observed proportion of marked fish in the catch, and the explanatory variable is sample area (lake or river). Each year of data represented an independent sample and the marked fraction was weighted by the total number of fish in the catch. We adjusted the variance of each estimate by a variance inflation factor (ϕ) to account for potential over-dispersion in the data and to make estimates as conservative as possible. We also used a simple Pearson's chi-square test as an alternative to test for differences in marked rates between the two different sampling areas (Zar 1999).

The percentage of marked fish in the catch was lower in lake sites compared with river sites for both groups of years (Figure 13), although the difference in marked rates was only significantly different in recent years (Logistic Regression, $P < 0.001$). In early years, the percentage of marked fish in the catch averaged 25% (95% CI = [16%, 41%]) in the lake site compared with 34% (95% CI = [27%, 42%] in the river site. The difference in the marked fraction between lake and river sites increased substantially in recent years, with the average percentage of marked fish in the lake catch averaging 43% (95% CI = [36%, 51%]) compared with 71% (95% CI = [68%, 73%]) for river fish. Chi-square analysis corroborated the results from the logistic regression model, indicating that the proportion of marked fish in the catch was significantly different between lake and river sites for recent years ($P < 0.001$), but not for early years.

This result is consistent with low sample sizes and the lower proportion of the population marked prior to 1997. Larger sample sizes and marked fractions in recent years increased the sampling power to discern differences.

Table 1. **Summary of marked and unmarked wild white sturgeon captured in Kootenay Lake (<= rkm 132) and Kootenai River between 1989 and 2008.**

	Lake				River				Total			
Year	Unmarked	Marked	Total	% Marked	Unmarked	Marked	Total	% Marked	Unmarked	Marked	Total	% Marked
1989	25	7	32	21.9%	185	30	215	14.0%	210	37	247	15.0%
1990	36	2	38	5.3%	64	33	97	34.0%	100	35	135	25.9%
1991	11	1	12	8.3%	31	14	45	31.1%	42	15	57	26.3%
1992	9	3	12	25.0%	36	16	52	30.8%	45	19	64	29.7%
1993	20	10	30	33.3%	61	23	84	27.4%	81	33	114	28.9%
1994	33	17	50	34.0%	61	36	97	37.1%	94	53	147	36.1%
1995	60	20	80	25.0%	95	60	155	38.7%	155	80	235	34.0%
1996	17	12	29	41.4%	60	53	113	46.9%	77	65	142	45.8%
1997	0	0	0	--	61	67	128	52.3%	61	67	128	52.3%
1998	20	10	30	33.3%	48	87	135	64.4%	68	97	165	58.8%
1999	5	9	14	64.3%	33	63	96	65.6%	38	72	110	65.5%
2000	12	6	18	33.3%	37	86	123	69.9%	49	92	141	65.2%
2001	2	6	8	75.0%	46	129	175	73.7%	48	135	183	73.8%
2002	9	5	14	35.7%	38	103	141	73.0%	47	108	155	69.7%
2003	13	6	19	31.6%	30	98	128	76.6%	43	104	147	70.7%
2004	17	8	25	32.0%	60	141	201	70.1%	77	149	226	65.9%
2005	2	2	4	50.0%	73	154	227	67.8%	75	156	231	67.5%
2006	6	8	14	57.1%	55	150	205	73.2%	61	158	219	72.1%
2007	16	19	35	54.3%	54	136	190	71.6%	70	155	225	68.9%
2008	16	10	26	38.5%	53	116	169	68.6%	69	126	195	64.6%
Average	16	8	25	36.8%	59	80	139	54.3%	76	88	163	51.8%

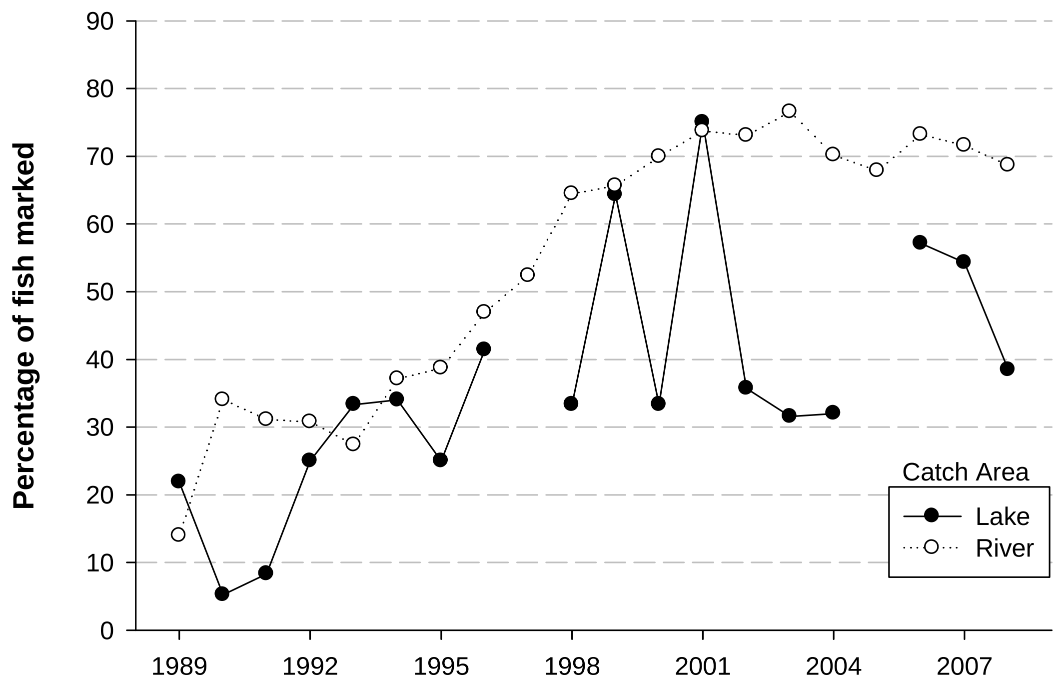

Figure 12. **Comparison of the percentage of marked adult white sturgeon out of the total number sampled in Kootenay Lake (< rkm 132) and Kootenai River from 1989 to 2008. Years with fewer than five total fish were excluded from this figure.**

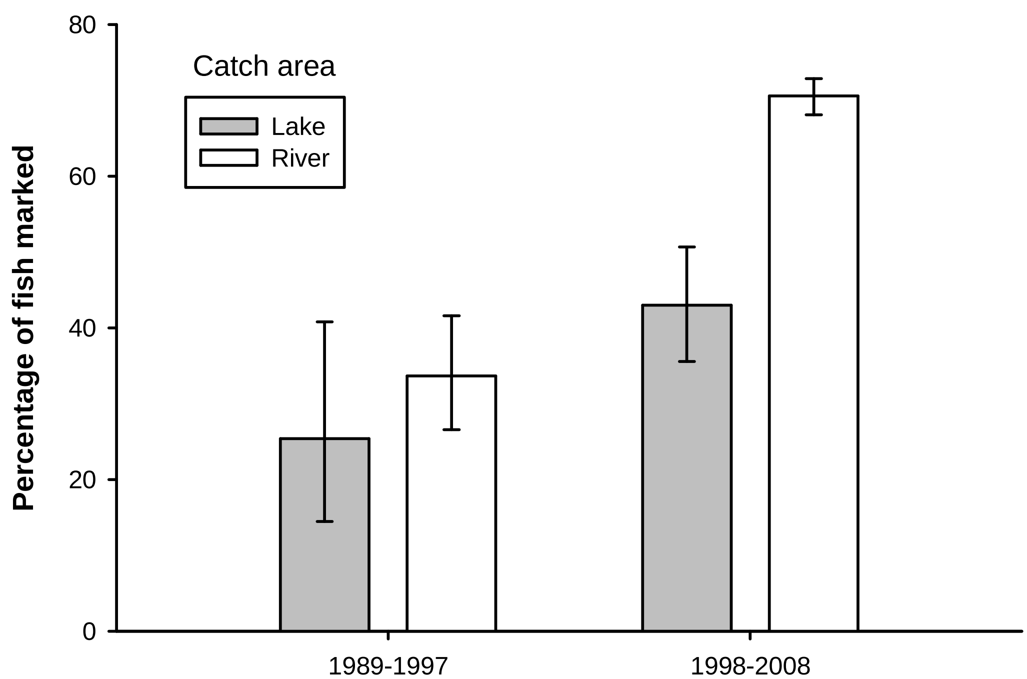

Figure 13. **Estimated percentage of adult white sturgeon out of the total number sampled in Kootenay Lake (<= rkm 132) and Kootenai River grouped by early sampling years (1989-1997) and recent years (1998-2008). Error bars denote 95% confidence intervals.**

Sampling effort

We summarized catch and sampling effort data from 1990 to 2008 for adult white sturgeon captured by angling and setlines to determine if there were any significant temporal trends or anomalous sampling years that might influence estimates of wild white sturgeon abundance. Sampling effort data was collected and provided by the Idaho Department of Fish and Game. We calculated the catch per unit effort (CPUE = catch / 24 effort hours) for each set, and then computed average CPUE and associated 95% confidence intervals for each year. Approximate 95% confidence intervals were based on an assumed lognormal distribution.

Catch per unit effort averaged 2.87 fish per day for angling gear and 0.61 fish per day for setlines (Table 2). CPUE was highly variable within years, and no apparent temporal trends were observed for either gear type (Figure 14). These data do not indicate any anomalous patterns in sampling effort that might substantially influence current abundance estimates. High catch rates in 1997 and 1998 are also associated with wide confidence intervals and do not represent a significant increase in relative sturgeon abundance.

Table 2. Catch and sampling effort and catch per unit effort (CPUE) for adult white sturgeon captured by the Idaho Department of Fish and Game in the Kootenai River using angling and setline gear from 1990 to 2008.

	Catch		Effort (24 hr days)		Average CPUE	
Year	Angling	Setline	Angling	Setline	Angling	Setline
1990	6	130	4.6	531.5	1.04	0.26
1991	16	41	9.1	115.2	1.74	0.47
1992	54	14	21.1	58.4	2.82	0.27
1993	61	19	12.5	56.9	7.06	0.30
1994	18	78	24.1	183.5	1.08	0.56
1995	16	31	11.8	126.5	3.39	0.59
1996	8	47	3.6	69.5	4.22	0.91
1997	7	65	4.4	96.4	1.42	1.90
1998	8	41	2.3	173.5	7.80	0.27
1999	11	37	4.7	161.6	2.68	0.22
2000	26	35	8.1	130.6	4.38	0.28
2001	10	63	7.0	149.5	2.12	0.63
2002	7	44	8.5	117.5	0.98	0.39
2003	34	48	19.8	128.4	2.69	0.37
2004	24	120	8.9	163.5	2.29	0.76
2005	67	89	24.9	140.7	2.34	0.76
2006	38	107	12.2	222.4	2.29	0.48
2007	36	91	18.4	186.7	2.71	1.06
2008	11	120	9.5	199.3	1.39	1.04
Average	24	64	11.3	158.5	2.87	0.61

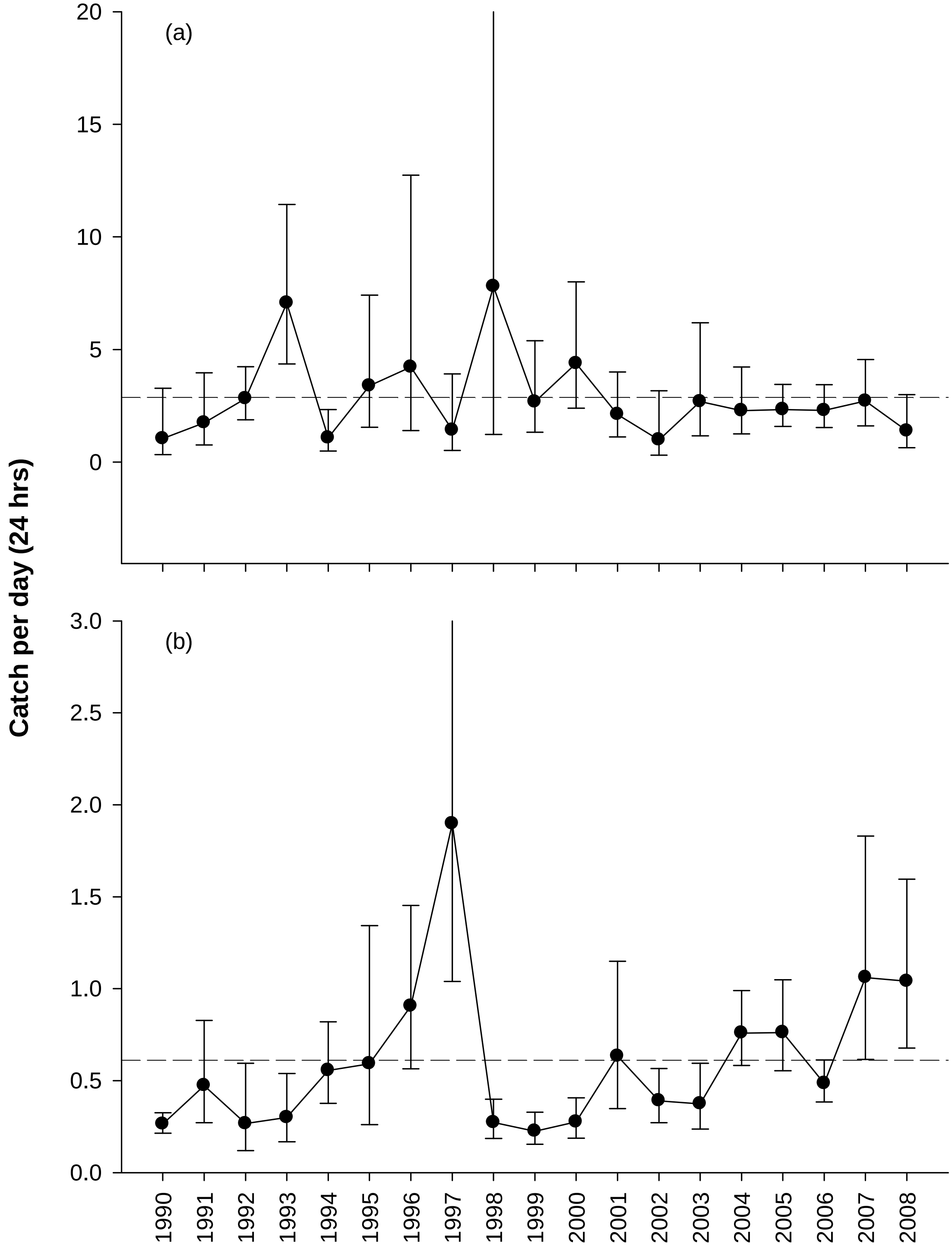

Figure 14. Catch per day (24 hours) using (a) angling with rod and reel, and (b) setlines from 1990 to 2008.

Potential non-random mixing bias in adult abundance estimates

Lower proportions of marked fish in lake samples indicated that the previously held assumption of complete mixing of marked and unmarked fish was likely violated, and consequentially, projections of adult abundance reported in Paragamian et al. (2005). To determine the extent to which previous abundance estimates may have been biased by incomplete mixing, we examined the sensitivity of abundance estimates to a range of assumed values for the percentage of mixing between marked and unmarked fish.

We present a hypothetical example based on an assumed marked fraction of 70% in river sites (Figure 12) and a total abundance estimate (assuming 100% mixing) of 500 fish. We used a simple Lincoln-Petersen estimator (Seber 1982) to generate population estimates and associated 95% confidence intervals. Although more rigorous statistical methods are available to estimate abundance for datasets involving multiple sampling events (e.g. Schnabel census) and open populations (e.g. Jolly-Seber), this approach is appropriate to illustrate the general relationship between mixing rates and population abundance and to approximate the level of bias in previous estimates of abundance for Kootenai River white sturgeon.

Abundance estimates were highly sensitive to the assumed rate of mixing between marked and unmarked fish, with abundance estimates increasing from 500 to 2,445 fish as the rate of mixing was decreased from 100% to 20% (Table 3; Figure 15). If we assume that the true proportion of marked fish in the catch is equal to the average value estimated from lake samples in recent years (i.e., 43%; Figure 13), then the implied percentage of mixing between marked and unmarked fish is approximately 60%. At this level of mixing, the actual abundance of adult white sturgeon was approximately 830 (Table 3). This equates to a 66% increase in abundance compared with the estimate generated under an assumption of 100% mixing (i.e., 500 fish). The error associated with the abundance estimates was also negatively related to the assumed percentage of mixing (Figure 15). That is, as the rate of mixing was decreased from 100% to 20%, the approximate 95% confidence bounds increased from about 29 to 698 fish.

Table 3. Summary of Lincoln-Petersen abundance estimates for a range of assumed values for the percentage of mixing between marked and unmarked adult white sturgeon in the Kootenai River.

Percentage	Proportion marked (m_2/n_2)		Period 1	Period 2				95% CI	
mixing	River	Lake	Catch (n_1)	Catch (n_2)	Marked (m_2)	Unmarked	Abundance (N)	LCI	UCI
100%	0.70	0.70	350	245	172	74	500	471	529
90%	0.70	0.63	350	245	154	91	555	515	594
80%	0.70	0.56	350	245	137	108	624	570	677
70%	0.70	0.49	350	245	120	125	712	639	785
60%	0.70	0.42	350	245	103	142	830	729	931
50%	0.70	0.35	350	245	86	159	994	849	1,140
40%	0.70	0.28	350	245	69	176	1,240	1,020	1,459
30%	0.70	0.21	350	245	51	194	1,645	1,284	2,006
20%	0.70	0.14	350	245	34	211	2,445	1,747	3,143

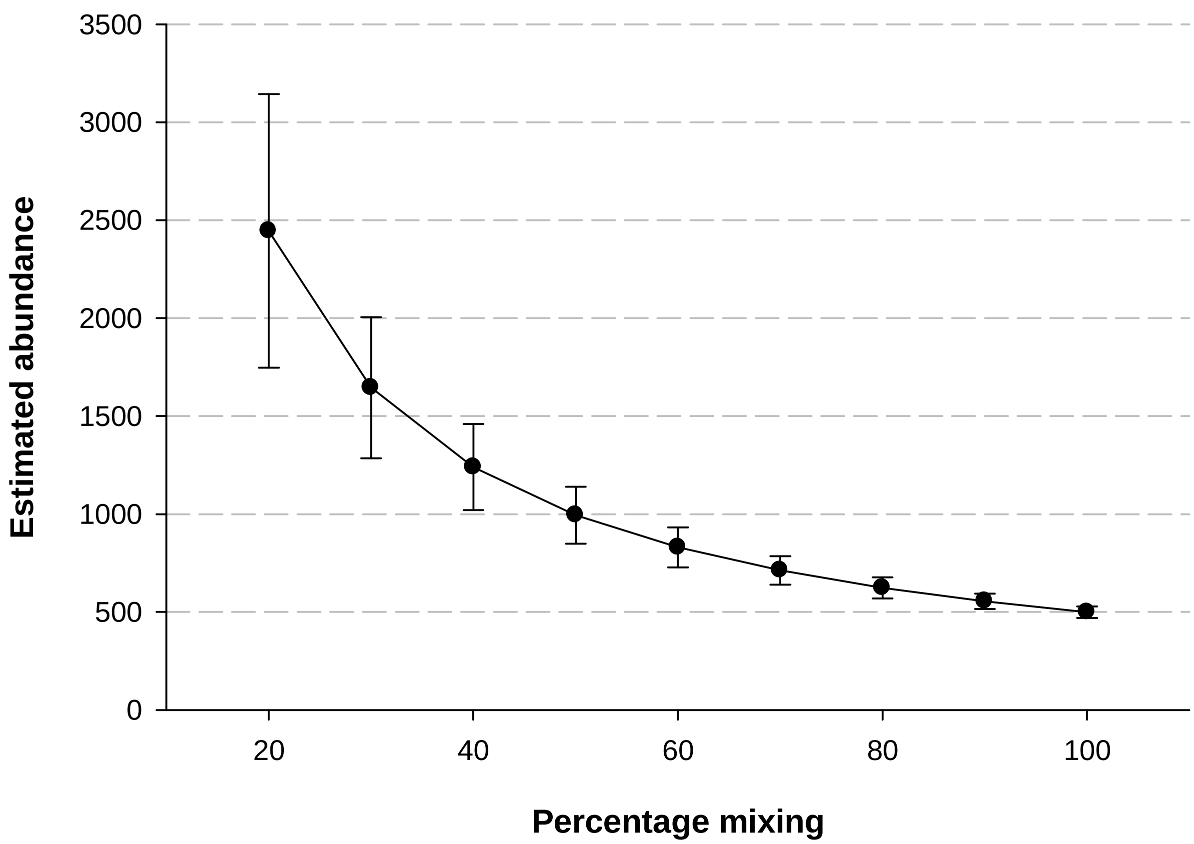

Figure 15. Relationship between abundance of adult white sturgeon in the Kootenai River and the percentage of mixing between marked and unmarked fish in the catch. Error bars represent approximate 95% confidence intervals.

Updated abundance estimates

We analyzed mark-recapture data for wild white sturgeon captured and tagged in the Kootenai River from 1977 to 2008 (Table 4). Abundance was estimated using an open-population Jolly-Seber approach implemented in POPAN-5 (Arnason et al. 1998). Initially we fit a death-only model that assumed no births or new entries to the population on the basis of observations of an extended interval of little or no natural recruitment (Anders et al. 2002). We then examined three additional capture-recapture models to explore the sensitivity of parameter estimates to different model assumptions. The three additional models included: 1) the full Jolly-Seber model which assumes time-dependent survival, capture probability, and births; 2) a constant survival model, which assumed time-dependent capture probability and births and constant survival; and 3) the death only model with constant survival. Births are defined as the number of new fish joining the population between samples *i* and *i* + 1 and present at *i* + 1. In this case, births may represent recruitment of individuals into the sampling area (i.e. lake fish entering the river), as opposed to newly born individuals. Results were compared with previous abundances estimates reported in Paragamian et al. (2005) based on the death-only model.

We evaluated model fit from the set of four candidate models using Akaike's information criterion (AIC). This information theoretic approach to model selection has been validated by simulation studies (Anderson et al. 1994; Burnham et al. 1995) and is strongly recommended for capture-recapture studies (Lebreton et al. 1992; Burnham and Anderson 2002).

A total of 2,082 wild white sturgeon were marked and released into the Kootenai River between 1977 and 2007 (Table 4). Of these, 1, 761 were subsequently recaptured. Sampling effort was sporadic prior to 1989, after which, captures of marked fish began to steadily increase. Abundance estimates were unavailable for 1984, 1985, and 1988 because no sampling occurred in these years. Additionally, abundance could not be estimated for the first (1977) or last year (2008) because estimates of capture probability require at least one sampling event prior to and after the period of interest (Williams et al. 2002).

The best-fitting capture-recapture model according to AIC was the full Jolly-Seber model (i.e., Model 2; Table 5). The difference in AIC (i.e., ΔAIC) between a given model and the AIC-selected best-fitting model (i.e., the model with the lowest AIC value) is frequently used to rank competing models and determine the level of empirical support for a given model (Burnham and Anderson 2002). In this case, the top competing model (i.e., Model 3) has a ΔAIC value of 189, indicating essentially no empirical support for Model 2 as the best-fitting model. Similarly, with ΔAIC values > 300, there is essentially no support for selection of Models 1 or 4 as the best fitting models in the candidate set. Thus, according to AIC alone, the full Jolly-Seber model which includes time-varying survival, capture, and recruitment rates is the best fitting model of the four candidate models.

Despite selection of the full Jolly-Seber model as the best fitting model according to AIC, the assumption that new individuals are recruiting to the population over time (i.e., new births) is likely flawed. Current evidence suggests that natural recruitment essentially ceased following completion of Libby Dam in 1972 (Anders et al. 2002), a finding that is corroborated by a recent evaluation of wild juvenile white sturgeon abundance in the Kootenai River (Pete Rust, IDFG, Pers. Comm.). Therefore, the Jolly Seber model wrongly assumes that a portion of the unmarked lake fish captured in the river represents new entries to the population, when in fact these fish have likely been residing in the lake undetected for many years. Consequentially, the Jolly-Seber model likely underestimates abundance. Because the death-only model provides more biologically reasonable constraints on recruitment, this model likely provides more accurate estimates of abundance, particularly in early years when the fraction of marked fish in the population was relatively low.

Abundance estimates generated from the death-only model ranged from 1,060 to 12,379 (mean = 3,464; S.D. = 3,218; Table 6). According to this model, the Kootenai white sturgeon population declined from approximately 12,000 in the late 1970's to about 1,000 in 2007 (Figure 16). Abundance estimates for early years (i.e., 1978-1987) were highly uncertain, with coefficients of variation (i.e., CV = S.E. (N) / N) ranging from 11 to 71% (mean CV = 33%). High variability in early abundance estimates was likely due to limited sample sizes and associated small proportions of marked fish in the population.

A comparison of abundance estimates from the death-only and full Jolly-Seber models indicated substantial variability in predicted abundance for the two different model types in early years, but similar estimates in more recent years (Figure 17). Abundance estimates from the death-only model from 1978 to 1987 averaged approximately five times higher than estimates from the full Jolly-Seber model (Figure 17). This large discrepancy in estimated abundance was related to model assumptions concerning recruitment as noted above. Given the high degree of uncertainty in early estimates of abundance for either model, it is not appropriate to draw decisive conclusions about the temporal variation in white sturgeon abundance during this time period. Fortunately, the two different models converged on similar estimates of abundance in recent years, suggesting that current abundance estimates are relatively robust to the choice of capture-recapture model.

These results indicate that a projected abundance of fewer than 500 fish in 2005 as reported in Paragamian et al. (2005) was likely biased low, and that the population of wild white sturgeon may be more stable than previously thought. Based on estimates from the death-only model, total population size for wild white sturgeon in the Kootenai River averaged 1,490 fish from 2002 to 2006. We excluded the 2007 abundance estimate from the current 5-year average because survival during 2006 was likely biased low (see survival section below), resulting in a biased abundance estimate for 2007.

Table 4. Summary of total releases and recaptures of marked wild white sturgeon in the Kootenai River from 1977 to 2008. Individuals captured multiple times in a single year are excluded.

	Marked	Recaptures																														
Year	Releases	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	Total
1977	96	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	0	0	1	0	1	1	0	0	11
1978	49		1	2	2	1	0	0	0	0	0	0	1	1	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	11
1979	19			2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
1980	163				18	10	0	0	0	0	0	0	5	4	3	1	2	3	4	7	4	4	1	2	2	2	1	4	3	4	2	3	89
1981	156					7	1	0	0	0	0	0	7	0	2	2	0	7	2	2	1	2	2	2	3	3	1	4	3	3	0	4	58
1982	63						0	0	0	0	0	0	6	1	0	0	3	3	3	1	7	4	3	4	3	5	3	4	0	3	5	3	61
1983	10							0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	4
1984	0								0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1985	0									0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1986	2										0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2
1987	10											0	1	0	0	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	1	0	7
1988	0												0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1989	209													24	6	6	13	18	29	14	15	15	18	10	23	16	11	18	15	23	21	13	308
1990	99														3	7	6	9	11	10	12	10	5	7	13	7	8	9	12	5	14	6	154
1991	42															1	2	6	4	3	4	2	3	6	4	4	4	6	6	5	4	5	69
1992	44																1	3	4	3	1	1	3	3	2	2	3	5	6	6	2	1	46
1993	81																	5	12	6	3	8	3	9	10	8	5	9	7	7	6	7	105
1994	130																		11	12	2	13	7	10	10	6	10	14	14	13	10	11	143
1995	177																			18	10	21	13	16	22	17	19	17	20	21	14	16	224
1996	100																				7	8	8	9	14	6	6	14	10	17	12	5	116
1997	61																					7	2	5	9	7	10	9	14	7	10	9	89
1998	68																						1	3	9	7	6	11	8	5	4	4	58
1999	38																							2	7	5	4	4	6	5	4	4	41
2000	49																								0	7	4	5	3	4	4	4	31
2001	47																									3	4	7	6	6	4	6	36
2002	47																										4	2	5	4	7	2	24
2003	41																											2	6	3	4	2	17
2004	77																												5	7	5	3	20
2005	75																													7	7	5	19
2006	60																														3	1	4
2007	69																															11	11
Total	2,082	0	1	4	21	20	2	0	0	0	0	0	21	31	14	18	28	60	81	77	67	96	70	90	131	106	104	144	151	156	143	125	1,761

Table 5. Summary of model comparison results for four capture-recapture models used to analyze abundance of wild white sturgeon in the Kootenai River from 1978 to 2007.

Model	Description	Log-Likelihood	Parameters	AIC	Delta AIC
1	Death-only	-7074.4	49	14247	313
2	Full Jolly-Seber	-6905.0	62	13934	0
3	Constant survival	-7019.5	42	14123	189
4	Death-only, constant survival	-7172.4	32	14409	475

Table 6. Abundance estimates and related parameters generated by the death-only model for wild white sturgeon in the Kootenai River from 1978 to 2007.

	Death-Only Model									
	Capture Probability		Survival		Births		Abundance		95% CI (N)	
Year	p	SE(p)	(phi)	(SE(phi))	(B)	(SE(B))	(N)	(SE(N))	Lower	Upper
1978	0.004	0.001	0.972	0.600	0	0	12,379	3,996	6,678	22,946
1979	0.002	0.001	0.713	0.383	0	0	12,026	6,333	4,560	31,714
1980	0.020	0.003	1.000	0.000	0	0	8,571	898	6,984	10,518
1981	0.021	0.003	0.779	0.171	0	0	8,567	898	6,980	10,514
1982	0.012	0.003	0.548	0.209	0	0	6,675	1,286	4,591	9,705
1983	0.003	0.001	0.909	0.709	0	0	3,655	1,206	1,946	6,865
1984	--	--	--	--	--	--	--	--	--	--
1985	--	--	--	--	--	--	--	--	--	--
1986	0.001	0.001	0.997	0.772	0	0	3,320	2,348	953	11,565
1987	0.003	0.001	0.837	0.269	0	0	3,310	1,047	1,807	6,062
1988	--	--	--	--	--	--	--	--	--	--
1989	0.083	0.007	0.904	0.081	0	0	2,771	163	2,470	3,109
1990	0.052	0.006	0.974	0.086	0	0	2,503	181	2,173	2,884
1991	0.023	0.003	1.000	0.000	0	0	2,438	141	2,177	2,730
1992	0.025	0.004	1.000	0.000	0	0	2,438	141	2,177	2,730
1993	0.045	0.005	0.870	0.066	0	0	2,438	141	2,177	2,730
1994	0.090	0.008	0.895	0.056	0	0	2,120	121	1,897	2,370
1995	0.136	0.009	1.000	0.000	0	0	1,897	76	1,754	2,052
1996	0.093	0.007	0.924	0.051	0	0	1,896	76	1,753	2,051
1997	0.073	0.007	1.000	0.000	0	0	1,752	85	1,592	1,927
1998	0.094	0.008	0.858	0.052	0	0	1,752	85	1,592	1,927
1999	0.072	0.007	1.000	0.000	0	0	1,503	74	1,366	1,655
2000	0.093	0.008	0.993	0.053	0	0	1,503	74	1,366	1,655
2001	0.119	0.009	1.000	0.000	0	0	1,492	61	1,377	1,617
2002	0.103	0.009	1.000	0.000	0	0	1,492	61	1,377	1,617
2003	0.097	0.008	1.000	0.000	0	0	1,492	61	1,377	1,617
2004	0.148	0.010	0.997	0.073	0	0	1,492	61	1,377	1,617
2005	0.152	0.014	1.000	0.000	0	0	1,488	105	1,296	1,708
2006	0.145	0.013	0.712	0.104	0	0	1,488	105	1,296	1,708
2007	0.201	0.029	--	--	--	--	1,060	141	818	1,373

Table 7. Abundance estimates and related parameters generated by the full Jolly-Seber model for wild white sturgeon in the Kootenai River from 1978 to 2007.

	Full Jolly-Seber Model									
	Capture Probability		Survival		Births		Abundance		95% CI (N)	
Year	p	SE(p)	(phi)	(SE(phi))	(B)	(SE(B))	(N)	(SE(N))	Lower	Upper
1978	0.033	0.036	0.956	0.578	119	2,110	1,496	1,647	261	8,575
1979	0.013	0.015	0.520	0.278	909	832	1,549	1,754	261	9,190
1980	0.098	0.017	0.951	0.198	0	0	1,712	271	1,258	2,330
1981	0.110	0.024	0.530	0.130	0	0	1,625	340	1,083	2,438
1982	0.097	0.027	0.518	0.150	454	593	861	221	524	1,413
1983	0.013	0.010	1.000	0.000	0	0	898	616	266	3,034
1984	--	--	--	--	--	--	--	--	--	--
1985	--	--	--	--	--	--	--	--	--	--
1986	0.002	0.002	1.000	0.000	798	680	897	616	265	3,034
1987	0.006	0.003	0.736	0.167	0	0	1,695	477	986	2,913
1988	--	--	--	--	--	--	--	--	--	--
1989	0.184	0.040	0.870	0.076	80	276	1,247	263	829	1,876
1990	0.112	0.021	0.958	0.096	295	268	1,165	197	838	1,620
1991	0.040	0.008	1.000	0.000	0	0	1,410	237	1,017	1,955
1992	0.044	0.009	0.979	0.106	278	249	1,410	237	1,017	1,955
1993	0.066	0.010	0.848	0.081	0	0	1,659	193	1,323	2,082
1994	0.135	0.017	0.873	0.054	235	114	1,408	148	1,146	1,729
1995	0.176	0.012	1.000	0.000	0	0	1,465	65	1,344	1,597
1996	0.121	0.010	0.894	0.048	0	0	1,464	65	1,343	1,596
1997	0.098	0.009	1.000	0.000	0	0	1,309	70	1,178	1,453
1998	0.125	0.011	0.840	0.063	0	0	1,309	70	1,178	1,453
1999	0.098	0.011	0.985	0.082	0	0	1,099	78	957	1,262
2000	0.128	0.013	0.935	0.061	0	0	1,083	74	948	1,237
2001	0.176	0.014	1.000	0.000	91	61	1,012	52	916	1,119
2002	0.139	0.013	1.000	0.000	28	78	1,103	72	971	1,253
2003	0.128	0.012	1.000	0.000	176	82	1,132	71	1,000	1,280
2004	0.169	0.014	0.897	0.067	74	76	1,308	76	1,166	1,466
2005	0.181	0.018	1.000	0.000	11	72	1,247	106	1,057	1,472
2006	0.172	0.017	0.632	0.094	116	53	1,258	98	1,080	1,466
2007	0.234	0.036	--	--	--	--	911	131	689	1,205

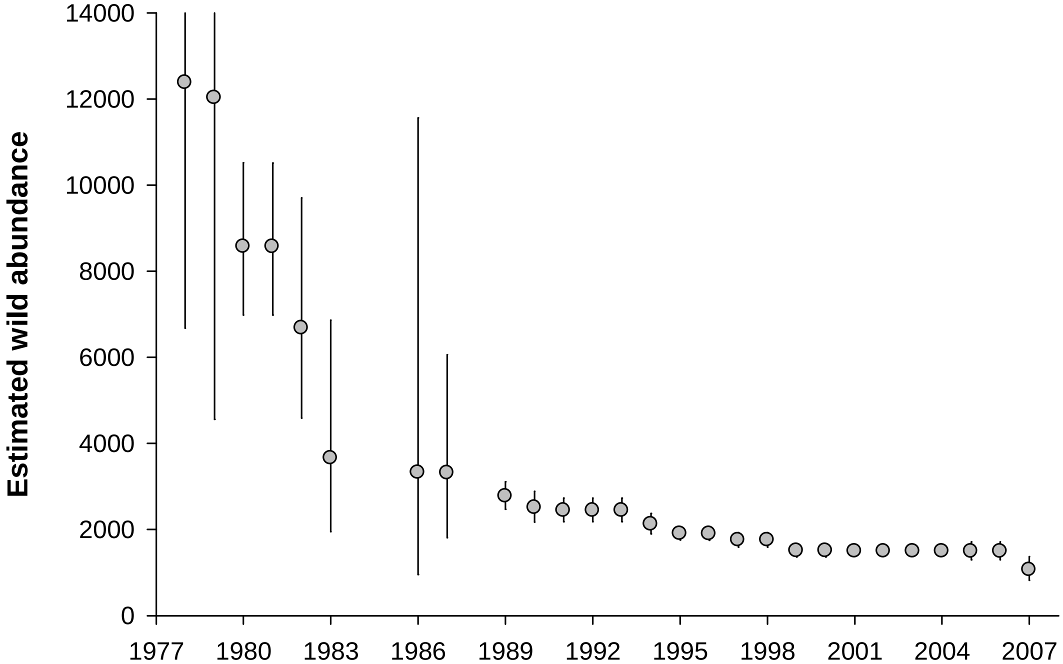

Figure 16. **Estimated abundance of wild white sturgeon in the Kootenai River from 1978 to 2007 based on the death-only model. Error bars represent approximate 95% confidence intervals.**

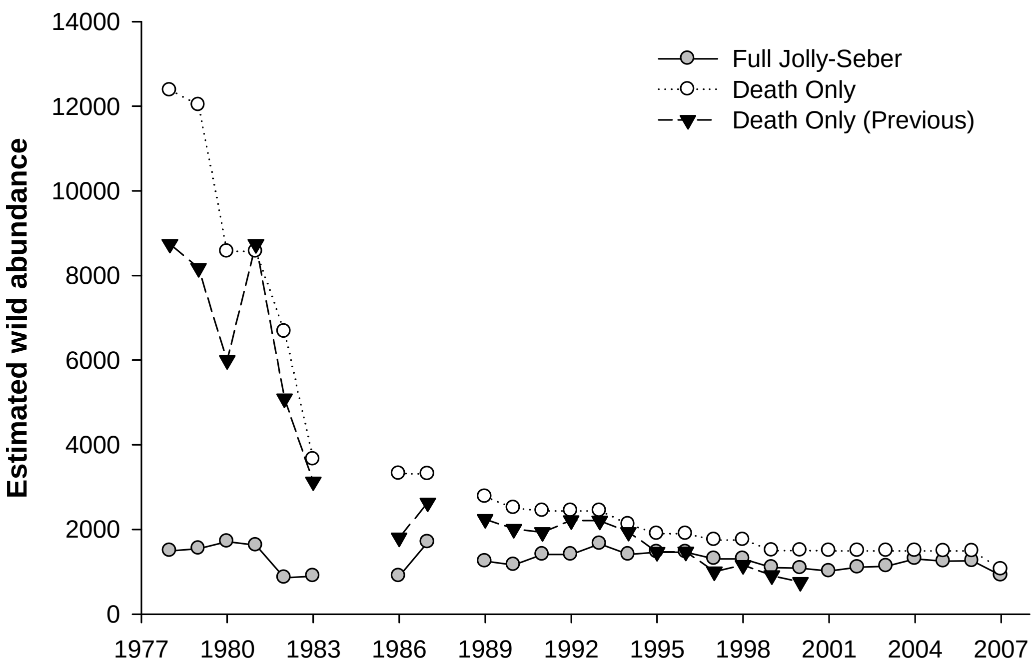

Figure 17. **Estimated abundance of wild white sturgeon in the Kootenai River from 1978 to 2007 for two competing models including the full Jolly-Seber model and the death-only model. Previous estimates of abundance from 1978 to 2000 generated from the death-only model (Paragamian et al. 2005) are shown for reference.**

Survival

We estimated survival rates for wild Kootenai River white sturgeon using acoustic telemetry data collected and provided the Idaho Department of Fish and Game (IDFG), and the British Columbia Ministry of Environment (BC MoE). Acoustically-tagged fish were monitored four times per year from 2003 to 2007, and once during 2008. Prior to estimating survival rates, we pooled the fish observations by year in order to simplify the analysis and to provide annual estimates of survival. We estimated survival rates for acoustically-tagged white sturgeon using a joint live and dead recoveries model (Burnham et al. 1993) implemented in program MARK. We examined four different biologically plausible capture-recapture models and used AIC to select the best fitting model among four candidate models. Models included 1) time-dependent survival and capture probability; 2) time-dependent survival and constant capture probability; 3) constant survival and time-dependent capture probability; and 4) constant survival and capture probability. These estimates were then compared with survival rates generated by POPAN5 for PIT-tagged fish and with estimates from catch-curve analyses (Paragamian et al. 2005) to determine how robust survival estimates are to different estimation methods.

Because several of the models in the candidate set were strong competing models according to AIC, we used a model averaging approach to estimate survival and capture probability. In this approach, we calculate a weighted average value for each parameter estimate, where each estimate is weighted by the model's AIC weight (Burnham and Anderson 2002). Estimated survival of acoustically-tagged white sturgeon from 2003 to 2006 was very high, with estimates ranging from 98.2 to 99.2% (mean = 98.8%; Table 8). These survival rates were very similar to the annual survival rate of 98% estimated from the same data using an alternative calculation method (Matt Neufeld, BC MoE, Pers. Comm.).

Comparatively, the geometric mean of annual survival rates estimated from wild PIT-tagged sturgeon from 1989 to 2005 was 96% (Table 6). We did not include the 2006 survival estimate in the average because simulation analysis in POPAN5 indicated that survival rates in the most recent years may be biased low by as much as 4.5%. Survival estimated from a catch-curve analysis for 1997-2001 was 94.4% (Paragamian et al. 2005).The discrepancy between mark-recapture estimates for PIT-tagged fish and the acoustic-telemetry results may have been driven by the inclusion of smaller fish in the Jolly-Seber estimate (i.e. adults and sub-adults were included in the analysis), while the acoustic telemetry estimate was based solely on adult fish. Similarly, survival rates estimated by catch-curve analysis were likely biased low by the decreasing trend in annual recruitment (Paragamian et al. 2005). Overall, these results suggest that wild white sturgeon in the Kootenai River are surviving at very high rates, regardless of which method is used to estimate survival.

Table 8. **Survival and capture probability of wild white sturgeon in the Kootenai River from 2003 to 2008 based on acoustic telemetry data.**

Year	Estimate	SE	LCI	UCI
Survival				
2003	0.992	0.008	0.976	1.000
2004	0.992	0.008	0.976	1.000
2005	0.982	0.020	0.859	0.998
2006	0.986	0.012	0.932	0.997
Capture probability				
2004	0.999	0.000	0.999	1.000
2005	0.999	0.000	0.999	1.000
2006	0.999	0.000	0.999	1.000
2007	0.999	0.000	0.999	1.000

Simulation Analysis to Explore Sources of Bias

We ran a series of simulation analyses to explore potential sources of bias in estimates of Kootenai white sturgeon abundance and survival. Specifically, we used the "SIMULATE" function in POPAN5 to generate a hypothetical death-only population with known survival rates and abundance. Simulations were designed to approximate the sampling design and observed abundance, survival and recapture rates for the Kootenai River white sturgeon population. We then explored various simulation scenarios consisting of known violations of model assumptions and compared the simulated results with known input values (i.e. expected values) to determine the magnitude of bias that might be expected under each scenario.

Simulations were seeded with an initial abundance of 10,000 fish, with no new recruits entering the population throughout the simulation period. We ran simulations over a 29 year period to be consistent with the actual period of record for sturgeon sampling in the Kootenai River (i.e., 1977-2008, minus 1984, 1985, and 1988). Survival rates were held fixed at 83% for the first nine years, and 96% thereafter to correspond with the geometric mean of survival estimates from the death-only model from 1978-1987 and from 1989 to 2005 (Table 6). Similarly, capture probability was set to 1% for the first nine years and 10% thereafter, corresponding with observed differences in capture rates between early and recent years. Each simulation was replicated 500 times, and average simulation results were compared with expected values to estimate bias.

We began by comparing simulation results from the death-only and full Jolly-Seber models with expected values to examine potential bias related to differences in model structure (i.e. births versus no-births). Because the true simulated population does not allow for new entries to the population over time (i.e., death-only), simulated estimates of abundance and survival generated from the death-only model should be more accurate than estimates from the full Jolly-Seber model, which allows for recruitment into the population. Indeed, the death-only model performed much better than the full Jolly-Seber model, with average estimates of abundance showing minimal positive bias during the first nine simulation years and no apparent bias thereafter (Figure 18). In contrast, the full Jolly-Seber model grossly underestimated abundance during early years of the simulation, but eventually converged on the true abundance level. These results highlight the dramatic differences in estimated abundance that can result from models with different assumptions regarding recruitment. A greater magnitude of bias during the early years of the simulation coincided with substantially lower capture probabilities and lower fractions of marked fish in the population. As noted above, the full Jolly-Seber model wrongly assumes that a portion of the unmarked population consists of new recruits, and therefore underestimates the true abundance. This effect might explain some of the variation between empirical estimates of abundance in the Kootenai River generated from the death-only and full Jolly-Seber models, although the actual amount of natural recruitment to the population is unknown.

Bias in survival estimates for both the full Jolly-Seber and death-only models varied substantially across years. Survival estimates were generally biased high during the early years of the simulation for both the death-only and full Jolly-Seber models, although the magnitude of bias was minimal (i.e., mean bias for both models for years 2-9 = 1.3%; Figure 19). During later simulation years (i.e., years 10-24), survival estimates were unbiased for both model types. However, survival rates were negatively biased during the last few years of the simulation, with the magnitude of bias increasing as the number of subsequent sampling periods decreased. Survival rates in the last estimable sampling period (i.e., period K-2 for a simulation with K sampling events) were biased by as much as 4.6 and 5.7% for the death-only and full Jolly-Seber models respectively. Similar declines in survival during the K-2 sampling period (i.e., 2006) were observed in the empirical mark-recapture estimates (Table 6 and Table 7). As a result, the abundance estimates in 2007 may have been biased low and should be interpreted with caution.

One important assumption associated with Jolly-Seber models is that all emigration from the study area is permanent. For populations like the Kootenai River, where individuals may spend considerable amounts of time in the lake where they are essentially not vulnerable to capture, the assumption about non-permanent emigration is violated and may result in biased abundance estimates. To explore the potential magnitude of this bias associated with non-permanent emigration, we simulated three different scenarios consisting of different levels of non-permanent emigration using the death-only model. Specifically, we simulated populations in which individuals were unavailable for capture (i.e., in the lake) for 25%, 50%, and 75% of the time. For example, at the 25% level, we specified that individuals spent three years in the river and one year in the lake.

The actual proportion of time that Kootenai River white sturgeon are unavailable for capture is unknown. If we consider the “lake” sampling area (i.e., lower river and estuary sites < rkm 132) as a “buffer” area, it is possible to estimate a lower bound for the proportion of emigrators following methods described in Arnason (1998). That is, the proportion of time spent out of the study area is estimated as the fraction of total recaptures in the buffer area out of all recaptures (not including the first capture). With the total number of recaptures in the lake totaling 161 out of a total of 1,756 recaptures, the estimated proportion of time that sturgeon are unavailable for capture is about 9%.

Increasing the proportion of time that individuals were unavailable for capture produced negative bias in the population estimates (Figure 20). In addition, the magnitude of the bias was greater in early simulation years, when simulated capture probabilities were significantly lower. Populations were essentially unbiased for simulations in which the proportion of time spent out of the study area was 25% or less. For simulations with 50% non-permanent emigration, the population estimates were negatively biased by approximately -10% (i.e., averaged from simulation year 10-28). For simulations with 75% non-permanent emigration, the population estimates were negatively biased by about -33% fish on average. Given the low estimate of 9% for the proportion of time that Kootenai River white sturgeon are unavailable for capture, it is unlikely that abundance estimates were significantly biased by non-permanent emigration into the lake.

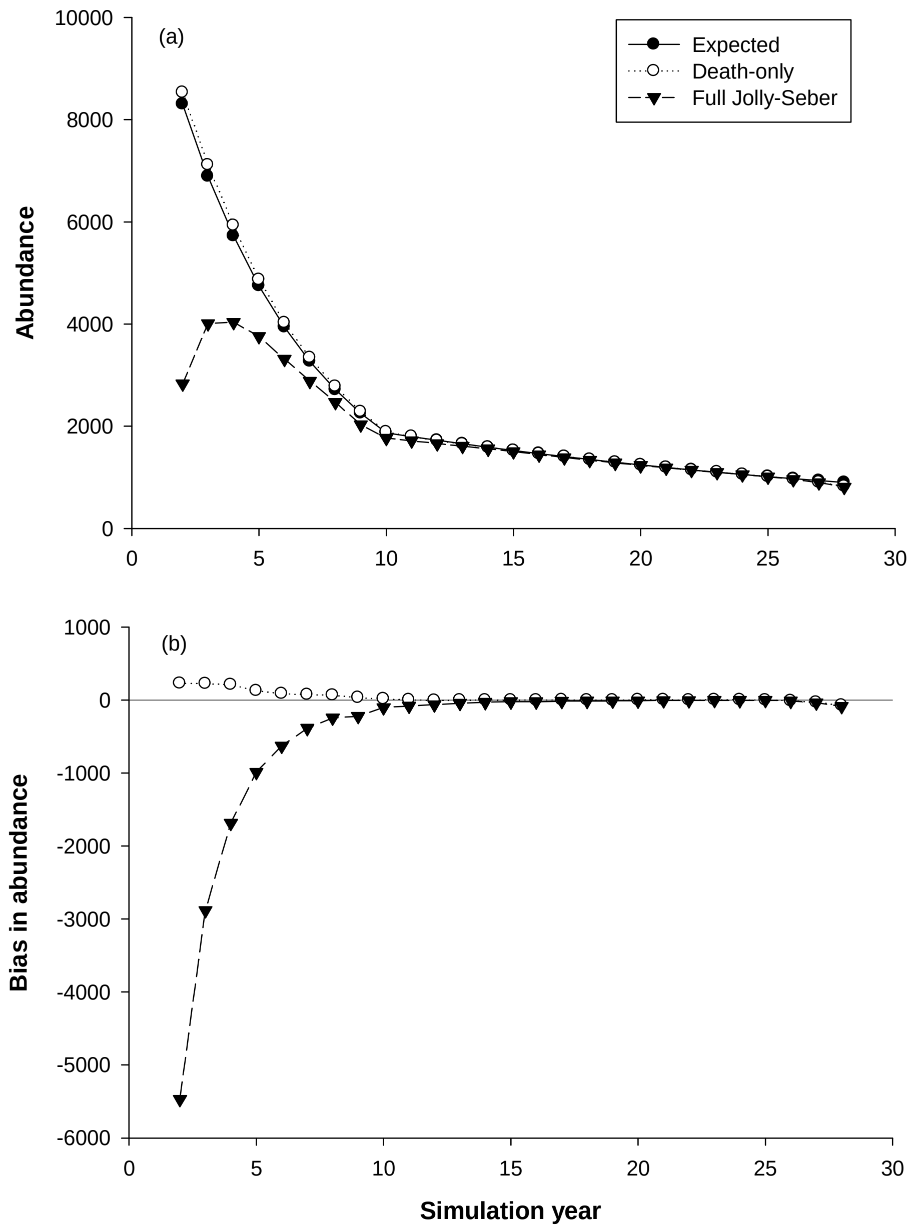

Figure 18. Simulated estimates of (a) abundance and (b) associated bias averaged over 500 replications for the death-only and full Jolly-Seber models.

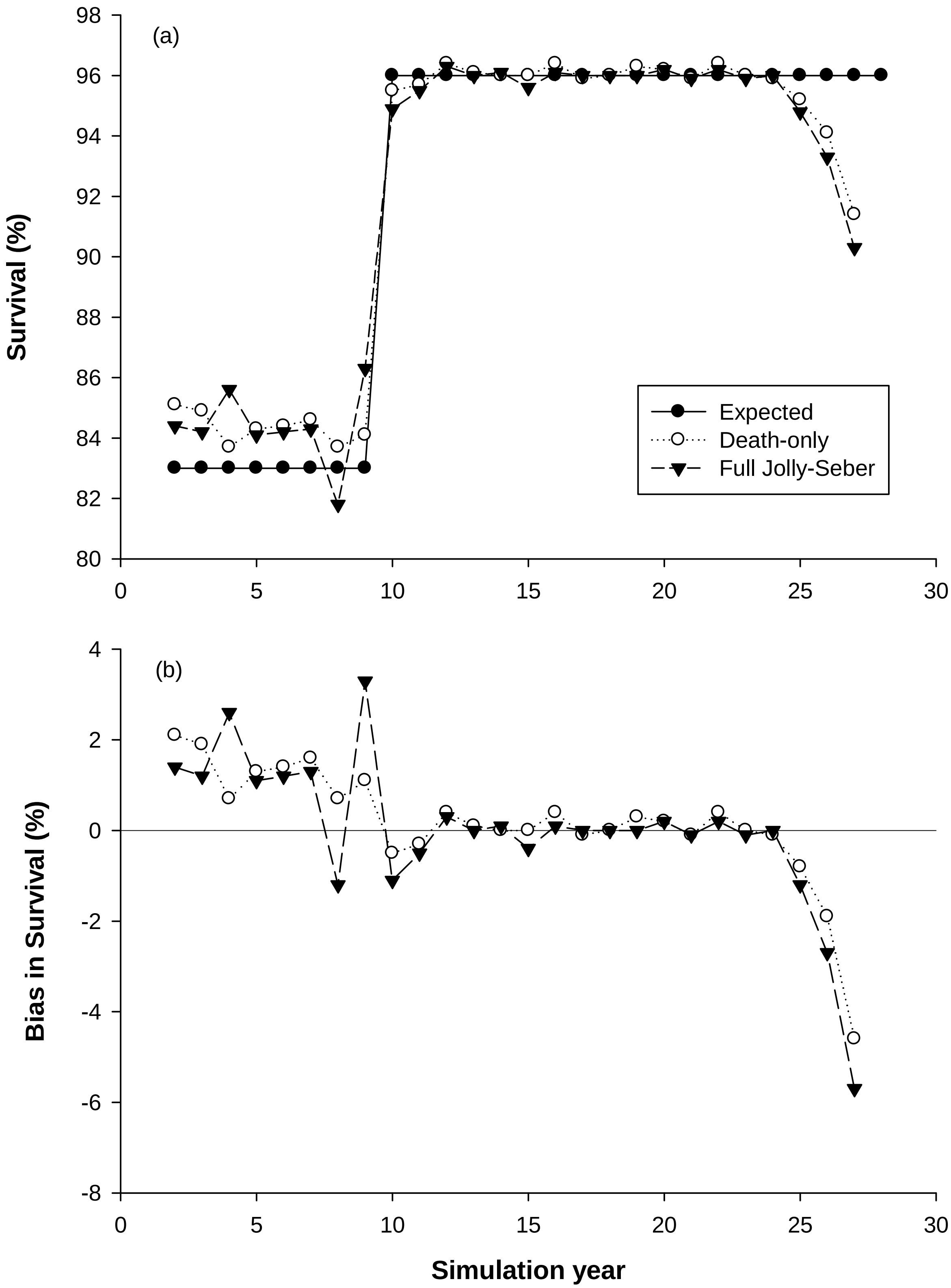

Figure 19. Simulated estimates of (a) survival and (b) associated bias averaged over 500 replications for the death-only and full Jolly-Seber models.

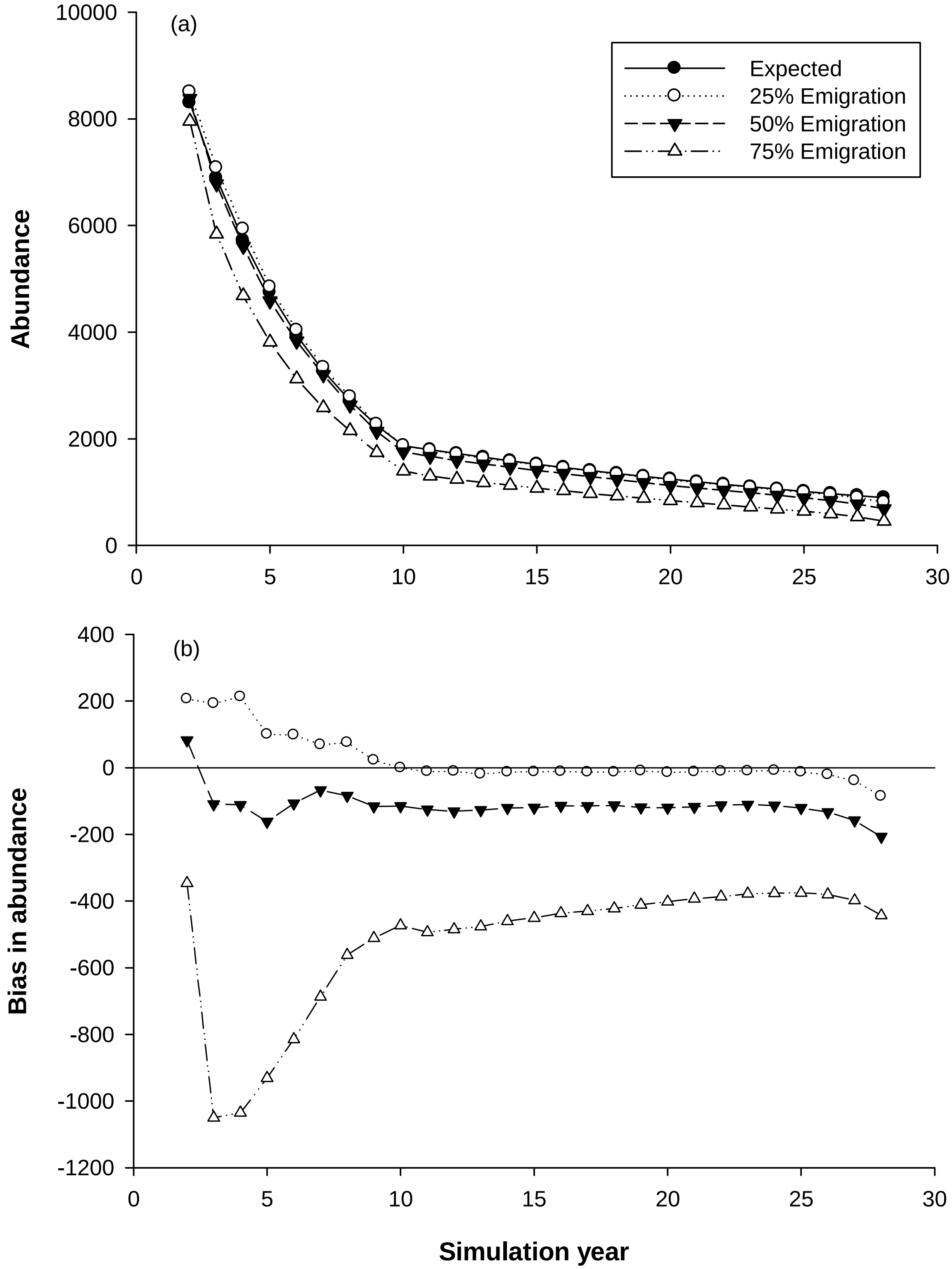

Figure 20. Simulated estimates of (a) abundance and (b) associated bias averaged over 500 replications for models with varying levels of non-permanent emigration (i.e., 25%, 50%, and 75%).

Natural Recruitment

Natural recruitment has been very low as evidenced by limited numbers of wild juveniles caught in gill nets since 1977. Catch data for wild juveniles in the Kootenai River was summarized and provided by Pete Rust of the Idaho Department of Fish and Game. Catch of wild juvenile white sturgeon (< 115 cm fork length) ranged from 0 to 82 (mean = 11) for capture years 1977 to 2008 (Figure 21). Catch by brood year ranged from 0 to 51 (mean = 5.3) for brood years 1957 to 2004 (Figure 22).

We used capture probabilities estimated from PIT-tagged hatchery-reared juveniles (Justice et al. 2009) to expand the juvenile catch to estimates of abundance. Estimates of wild juvenile abundance were limited to years for which capture probability estimates were available (i.e., 1993 to 2005). Wild juvenile abundance ranged from 13 to 200 (mean = 58) for capture years 1993 to 2005 (Table 9). Of keen interest for modeling purposes is the number of age-1 juveniles produced in each year. Unfortunately, we do not have sufficient data to accurately estimate the age frequency distribution for wild juveniles, and thereby calculate the fraction of total juveniles composed of age-1 fish. For model simulations (see Population Projections below), we assumed a constant recruitment rate of 10 age-1 fish per year.

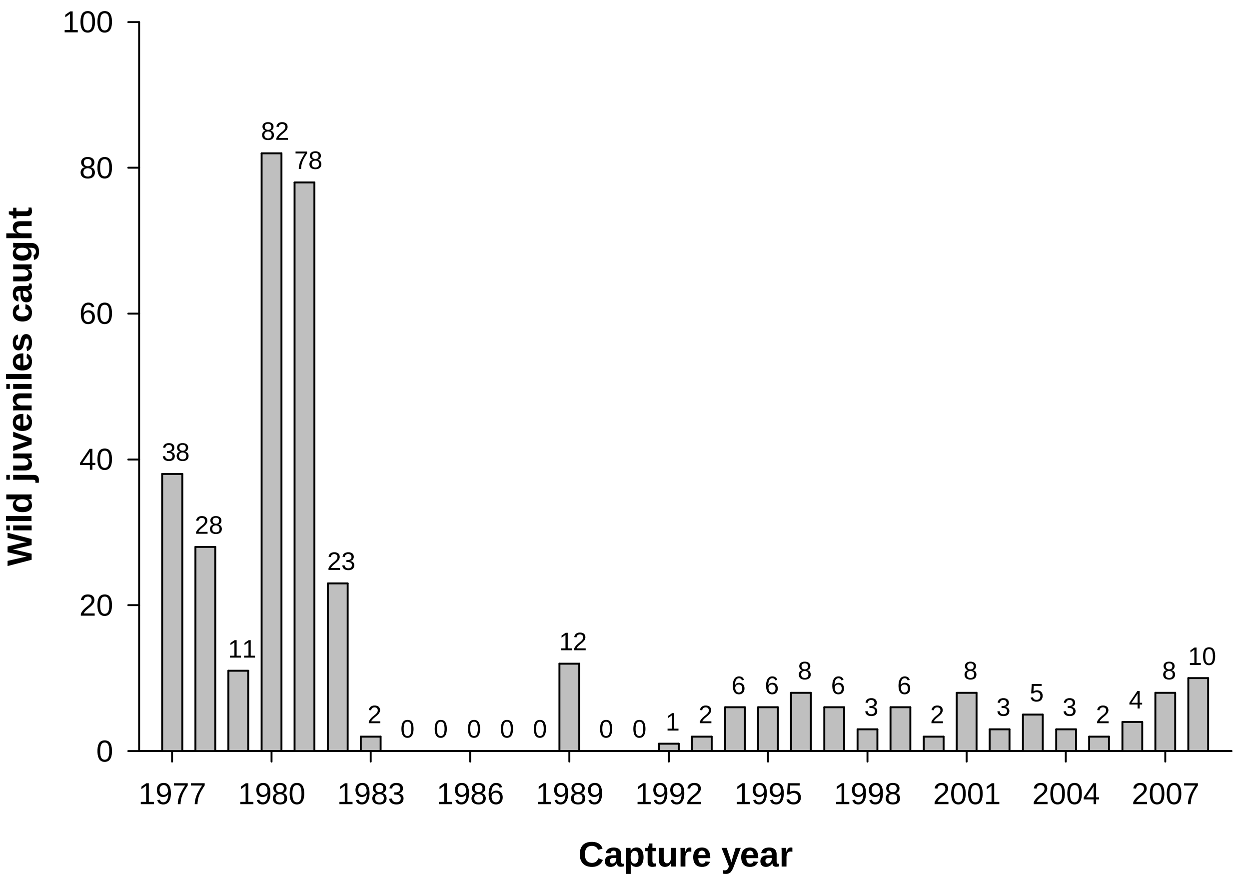

Figure 21. Number of wild juvenile white sturgeon captured in the Kootenai River from 1975 to 2008 by year of capture.

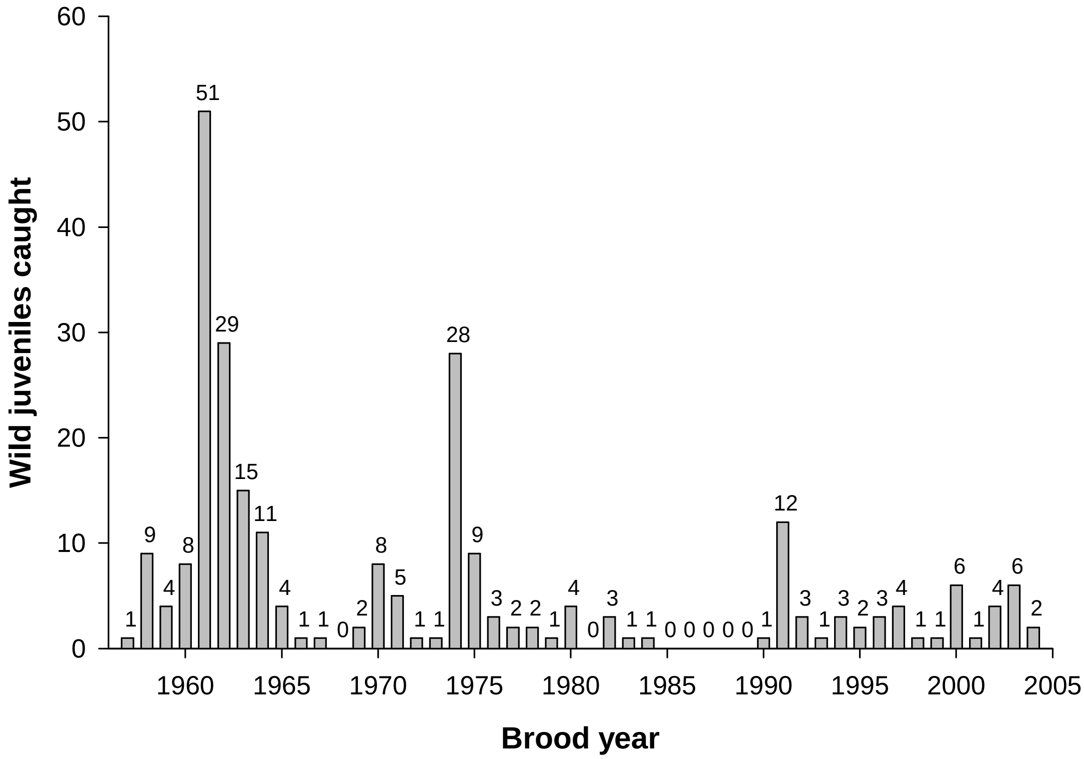

Figure 22. Number of wild juvenile white sturgeon captured in the Kootenai River from 1975 to 2008 by brood year

Table 9. Estimated abundance of wild juvenile white sturgeon in the Kootenai River from 1993 to 2005. Capture probability was estimated from PIT-tagged juvenile hatchery fish as reported in Justice et al. (2009).

Year	Capture probability	Number captured	Estimated abundance
1993	0.01	2	200
1994	--	6	--
1995	0.17	6	35
1996	0.27	8	30
1997	0.14	6	43
1998	0.12	3	25
1999	0.12	6	50
2000	0.15	2	13
2001	0.14	8	57
2002	0.07	3	43
2003	0.05	5	100
2004	0.06	3	50
2005	0.04	2	50
Average	0.11	5	58

Population projections

We used a simple age-structured population model to project future population size and female spawner abundance of wild and hatchery-reared white sturgeon in the Kootenai River as originally described in Paragamian et al. (2005). The model calculates a series of age-specific parameters such as length, growth, survival, and sexual maturity using the input parameters outlined in Table 10. Model parameters were updated to reflect current information about survival rates and stocking numbers. Model simulations began in 1989 and were run for 100 years. Release numbers and survival rates from 1989 to 2006 were based on actual release numbers and estimated survival rates from Justice et al. (2009). Release numbers and survival rates were held constant for the remainder of the simulation period. An example of the life table used in model simulations is provided in Table 11.

Table 10. Summary of model parameters and values, definitions and equations used to project population trajectories.

Variable or parameter	Definition	Value: Current	Value: Previous
$N_{x,t,o}$	Age-specific number of fish in population at time t ; = $(N_{x-1,t-1})(S_x)$		
x	Age		
t	Year		
o	Origin (wild or hatchery)		
$t=1$	Initial year	1989	1980
$N_{t,w}$	Initial wild population size	2,771	6,813
R_h	Annual hatchery recruitment	18,000	12,000
R_w	Annual wild recruitment	10	10
S_x	Age-specific annual rate of survival; = $1 - (m_x + n_x - m_x{\cdot}n_x)$		
m_x	Exploitation (harvest mortality rate)[a]	0	0.105
n_x	Natural mortality rate		
	First year after hatchery release	0.55	0.40
	Age 1 - 3	0.12	0.10
	Age 4 - 10	0.04	0.10
	Age 11+	0.04	0.087
L_x	Length at age: = $L_\infty \cdot \{1-\exp[-k(x-t_0)]\}$		
L_∞	Von Bertalanffy equation length at infinity	276	276
k	Von Bertalanffy equation slope parameter	0.028	0.0145
t_0	Von Bertalanffy equation intercept parameter	-2	-3.12
W_x	Weight at age; = $(a_w)(L_x)^{bw}$		
a_w	Length-weight equation coefficient for Upper Columbia sturgeon populations	4.10E-06	4.10E-06
b_w	Length-weight equation exponent for Upper Columbia sturgeon populations	3.12	3.12
ps_x	Proportion of the population of females of each age class that spawn in any year; = $1 - [1/(1+C_\infty{\cdot}\vartheta)]$ for $L_x \le \mu$, = $1 - \{1/[1+C_\infty{\cdot}(1-\vartheta)]\}$ for $L_x > \mu$		
C_∞	Maximum proportion of spawning females	0.333	0.333
ϑ	Cumulative normal distribution function dependent variable; = $1/(2\pi)^{0.5}{\cdot}\exp[-(L_x-\mu)^2]{\cdot}\sum b_i\{1+p\lvert(L_x-\mu)/\sigma\rvert\}^{1-i}$		
pf	Proportion of the population that is female	0.50	0.50
μ	Mean length of females at sexual maturity (cm)	140	140
σ^2	Variance about mean length of females at sexual maturity	20	20
$b_1, \ldots, b_5$	Constants	0.31938153	0.31938153
		-0.356563782	-0.356563782
		1.781477937	1.781477937
		-1.821255978	-1.821255978
		1.330274429	1.330274429
p	Constant	0.2316419	0.2316419

[a] *Exploited size range = 92-183 cm; Only applies to years prior to 1989.*

Table 11. Example of the life table from the population model.

age	fl cm	fl in	tl cm	tl in	wt kg	wt lb	growth incr cm	Ws kg	Wr optimur	natl surv	exploit	survival annual	survival net to age	sex p fem	fem mat p
1	22.2	8.8	25.3	10.0	0.1	0.1		0.1	106%	0.880	0.000	0.880	1.000	0.5	0.000
2	29.2	11.5	33.3	13.1	0.2	0.3	7.0	0.1	103%	0.880	0.000	0.880	0.880	0.5	0.000
3	36.1	14.2	41.0	16.2	0.3	0.7	6.8	0.3	100%	0.880	0.000	0.880	0.774	0.5	0.000
4	42.7	16.8	48.6	19.1	0.5	1.1	6.6	0.5	98%	0.960	0.000	0.960	0.681	0.5	0.000
5	49.1	19.3	55.9	22.0	0.8	1.7	6.4	0.8	97%	0.960	0.000	0.960	0.654	0.5	0.000
6	55.4	21.8	63.0	24.8	1.1	2.5	6.3	1.2	96%	0.960	0.000	0.960	0.628	0.5	0.000
7	61.5	24.2	70.0	27.5	1.6	3.4	6.1	1.7	95%	0.960	0.000	0.960	0.603	0.5	0.000
8	67.4	26.5	76.7	30.2	2.1	4.6	5.9	2.2	94%	0.960	0.000	0.960	0.579	0.5	0.000
9	73.2	28.8	83.3	32.8	2.7	5.9	5.8	2.9	93%	0.960	0.000	0.960	0.556	0.5	0.000
10	78.8	31.0	89.6	35.3	3.4	7.4	5.6	3.7	92%	0.960	0.000	0.960	0.533	0.5	0.000
11	84.2	33.2	95.8	37.7	4.2	9.2	5.4	4.6	91%	0.960	0.000	0.960	0.512	0.5	0.000
12	89.5	35.2	101.9	40.1	5.0	11.1	5.3	5.6	91%	0.960	0.000	0.960	0.492	0.5	0.000
13	94.7	37.3	107.7	42.4	6.0	13.2	5.1	6.7	90%	0.960	0.000	0.960	0.472	0.5	0.000
14	99.7	39.2	113.4	44.7	7.1	15.5	5.0	7.9	90%	0.960	0.000	0.960	0.453	0.5	0.016
15	104.5	41.2	119.0	46.8	8.2	18.0	4.9	9.2	89%	0.960	0.000	0.960	0.435	0.5	0.026
16	109.3	43.0	124.3	49.0	9.4	20.7	4.7	10.6	89%	0.960	0.000	0.960	0.418	0.5	0.040
17	113.9	44.8	129.6	51.0	10.7	23.5	4.6	12.1	88%	0.960	0.000	0.960	0.401	0.5	0.059
18	118.3	46.6	134.7	53.0	12.1	26.5	4.5	13.7	88%	0.960	0.000	0.960	0.385	0.5	0.080
19	122.7	48.3	139.6	55.0	13.5	29.7	4.4	15.4	87%	0.960	0.000	0.960	0.369	0.5	0.104
20	126.9	50.0	144.4	56.9	15.0	33.0	4.2	17.2	87%	0.960	0.000	0.960	0.355	0.5	0.129
21	131.0	51.6	149.1	58.7	16.6	36.4	4.1	19.1	87%	0.960	0.000	0.960	0.340	0.5	0.153
22	135.1	53.2	153.7	60.5	18.2	40.0	4.0	21.0	87%	0.960	0.000	0.960	0.327	0.5	0.175
23	138.9	54.7	158.1	62.3	19.9	43.7	3.9	23.0	86%	0.960	0.000	0.960	0.314	0.5	0.195
24	142.7	56.2	162.4	63.9	21.6	47.6	3.8	25.1	86%	0.960	0.000	0.960	0.301	0.5	0.213
25	146.4	57.6	166.6	65.6	23.4	51.5	3.7	27.3	86%	0.960	0.000	0.960	0.289	0.5	0.230
26	150.0	59.0	170.7	67.2	25.2	55.5	3.6	29.5	86%	0.960	0.000	0.960	0.278	0.5	0.247
27	153.5	60.4	174.6	68.8	27.1	59.6	3.5	31.8	85%	0.960	0.000	0.960	0.266	0.5	0.262
28	156.8	61.8	178.5	70.3	29.0	63.8	3.4	34.1	85%	0.960	0.000	0.960	0.256	0.5	0.276
29	160.1	63.0	182.2	71.7	31.0	68.1	3.3	36.5	85%	0.960	0.000	0.960	0.246	0.5	0.287
30	163.3	64.3	185.9	73.2	32.9	72.4	3.2	38.9	85%	0.960	0.000	0.960	0.236	0.5	0.297
31	166.4	65.5	189.4	74.6	34.9	76.8	3.1	41.3	85%	0.960	0.000	0.960	0.226	0.5	0.305
32	169.5	66.7	192.9	75.9	36.9	81.3	3.0	43.8	84%	0.960	0.000	0.960	0.217	0.5	0.312
33	172.4	67.9	196.2	77.2	39.0	85.8	2.9	46.3	84%	0.960	0.000	0.960	0.209	0.5	0.317
34	175.3	69.0	199.5	78.5	41.0	90.3	2.9	48.8	84%	0.960	0.000	0.960	0.200	0.5	0.321
35	178.1	70.1	202.6	79.8	43.1	94.8	2.8	51.4	84%	0.960	0.000	0.960	0.192	0.5	0.324
36	180.8	71.2	205.7	81.0	45.2	99.4	2.7	53.9	84%	0.960	0.000	0.960	0.185	0.5	0.326
37	183.4	72.2	208.7	82.2	47.3	104.0	2.6	56.5	84%	0.960	0.000	0.960	0.177	0.5	0.328
38	185.9	73.2	211.6	83.3	49.3	108.6	2.6	59.1	83%	0.960	0.000	0.960	0.170	0.5	0.330
39	188.4	74.2	214.4	84.4	51.4	113.2	2.5	61.7	83%	0.960	0.000	0.960	0.163	0.5	0.331
40	190.9	75.1	217.2	85.5	53.5	117.8	2.4	64.3	83%	0.960	0.000	0.960	0.157	0.5	0.331
41	193.2	76.1	219.9	86.6	55.6	122.3	2.4	66.9	83%	0.960	0.000	0.960	0.150	0.5	0.332
42	195.5	77.0	222.5	87.6	57.7	126.9	2.3	69.5	83%	0.960	0.000	0.960	0.144	0.5	0.332
43	197.7	77.8	225.0	88.6	59.8	131.5	2.2	72.1	83%	0.960	0.000	0.960	0.139	0.5	0.333
44	199.9	78.7	227.5	89.5	61.8	136.0	2.2	74.6	83%	0.960	0.000	0.960	0.133	0.5	0.333
45	202.0	79.5	229.8	90.5	63.9	140.5	2.1	77.2	83%	0.960	0.000	0.960	0.128	0.5	0.333
46	204.0	80.3	232.2	91.4	65.9	145.0	2.0	79.8	83%	0.960	0.000	0.960	0.123	0.5	0.333
47	206.0	81.1	234.4	92.3	67.9	149.5	2.0	82.3	83%	0.960	0.000	0.960	0.118	0.5	0.333
48	207.9	81.9	236.6	93.2	69.9	153.9	1.9	84.8	82%	0.960	0.000	0.960	0.113	0.5	0.333
49	209.8	82.6	238.8	94.0	71.9	158.3	1.9	87.3	82%	0.960	0.000	0.960	0.109	0.5	0.333
50	211.6	83.3	240.9	94.8	73.9	162.6	1.8	89.8	82%	0.960	0.000	0.960	0.104	0.5	0.333

Projected abundance of wild and hatchery adult white sturgeon differed substantially from previous estimates reported in Paragamian et al. (2005). Specifically, the projected number of hatchery adults in the population after 100 years increased from approximately 3,000 fish for previous estimates, to nearly 70,000 fish under current assumptions of survival and recruitment (Figure 23). This dramatic difference was due to lower estimated mortality rates for juvenile and adult life stages and a projected increase in annual hatchery releases from 12,000 to 18,000 (Table 10). The mortality estimates used in the model represent the best available information derived from current analyses of survival of hatchery-reared juveniles (Justice et al. 2009) and from recent analyses of PIT- and Acoustic-tagged wild adult sturgeon (see survival section above).

Under current model assumptions, the predicted abundance of wild adult white sturgeon declined from approximately 2,363 in 1989 to only 1,217 in 2009. If current rates of decline continue, the population will be expected to fall below 500 fish by 2033 and may decline to as few as 70 fish by 2080. Substantial numbers of adult hatchery fish are projected to begin recruiting to the population by the year 2020, after which, the hatchery population should increase rapidly to over 10,000 fish by the year 2032. Clearly, the upper limit on the number of adult white sturgeon that can survive in the Kootenai River is a critical uncertainty that is largely dependent on the availability of suitable rearing and spawning habitats. A projected abundance of 70,000 hatchery adults after 100 years is likely an overestimate because it assumes no density-dependence and continuous production of hatchery fish.

Predicted abundance of wild female spawners declined from 379 in 1989 to 202 in 2009, with numbers expected to reach fewer than 50 fish by 2046 (Figure 24). In contrast, hatchery female spawners are projected to increase rapidly from only 8 fish in 2009 to over 10,000 in 2056.

Updated model simulations suggest that a much greater proportion of the population will be composed of adults after 100 years than previously predicted (Figure 25). For example, adults comprised approximately 34% of the population in 2079 compared with only 3.8% for previous model simulations in the same year. This substantial difference was due primarily to the lower mortality estimates for adults used in current model simulations.

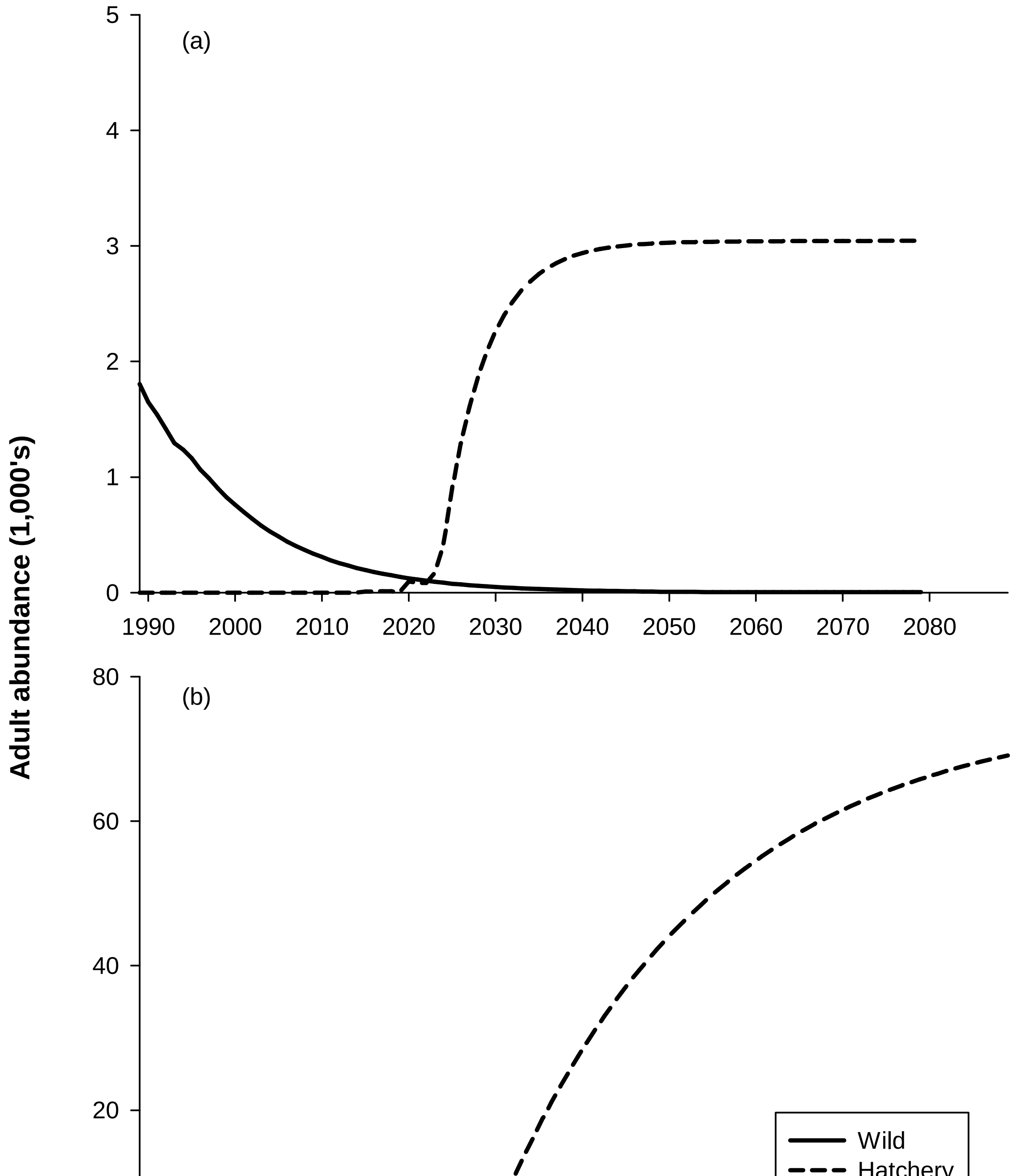

Figure 23. Simulated abundance of wild and hatchery adult white sturgeon in the Kootenai River using (a) previous model inputs from Paragamian et al. (2005), and (b) current model inputs.

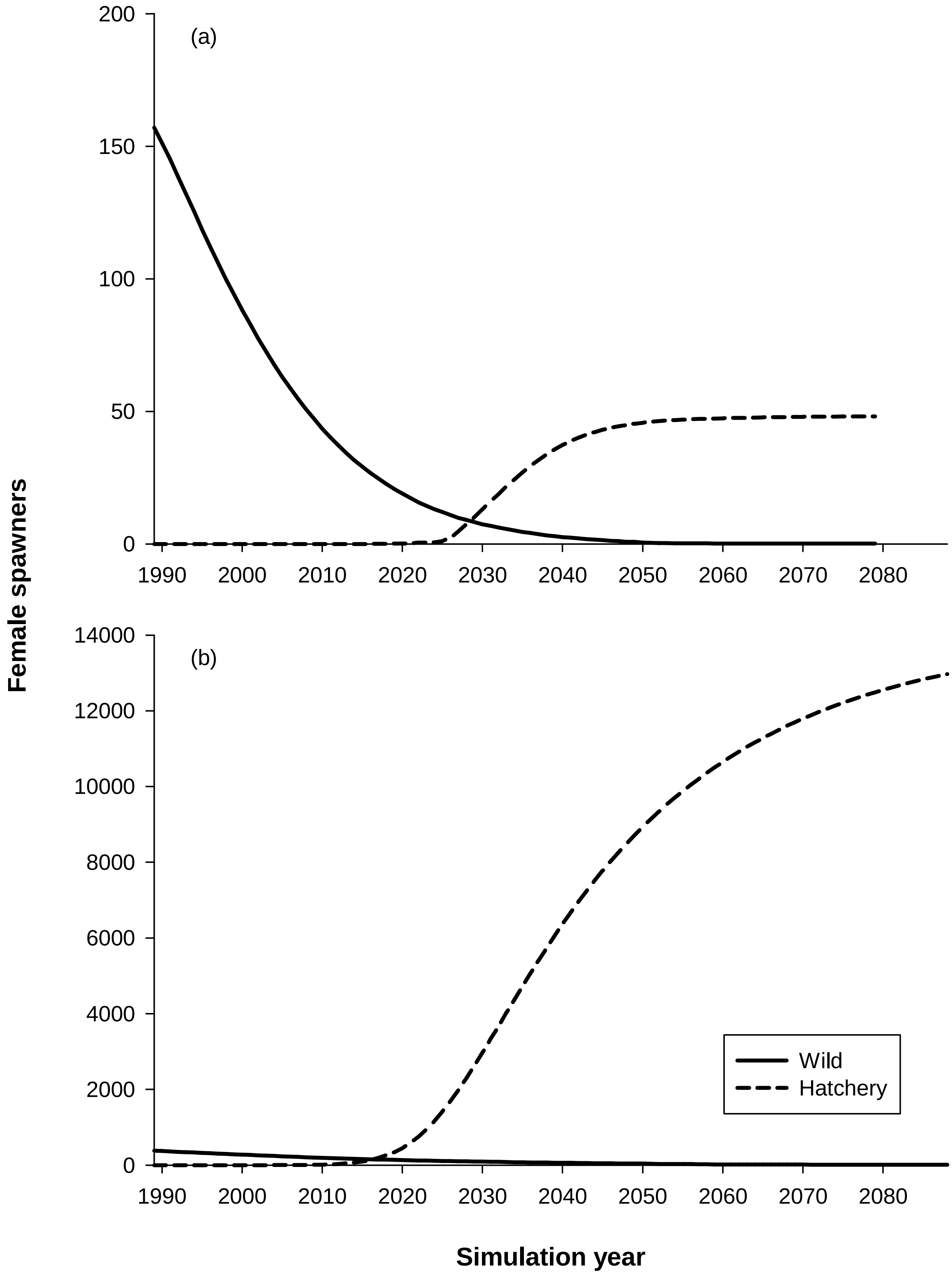

Figure 24. Simulated abundance of wild and hatchery white sturgeon female spawners in the Kootenai River using (a) previous model inputs from Paragamian et al. (2005), and (b) current model inputs.

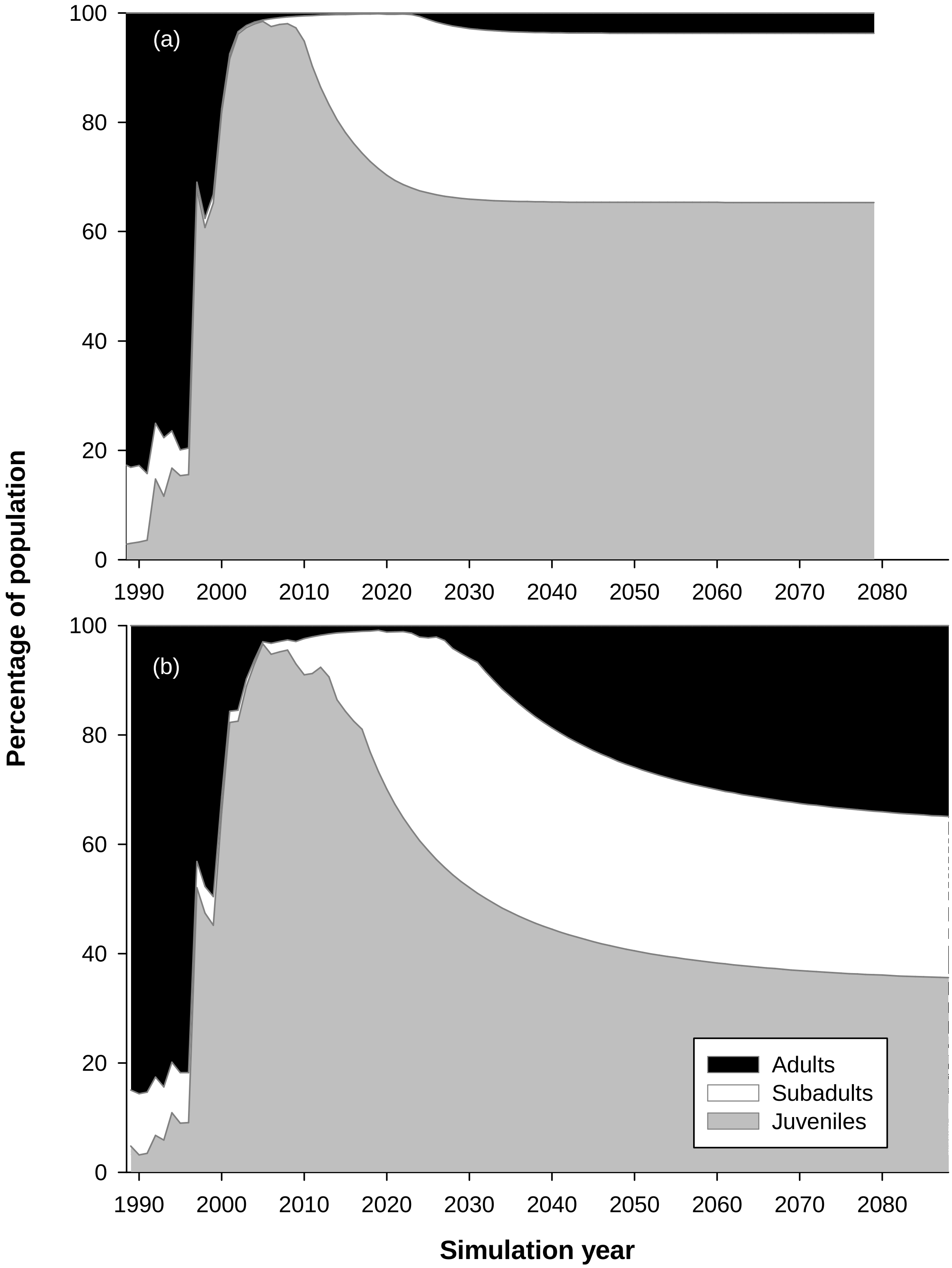

Figure 25. Simulated proportions of wild and hatchery adult (ages > 24), subadult (ages 11-24), and juvenile (ages < 11) white sturgeon in the Kootenai River using (a) previous model inputs from Paragamian et al. (2005), and (b) current model inputs.

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