

Status, Population Dynamics, and Future Prospects of the Endangered Kootenai River White Sturgeon Population with and without Hatchery Intervention

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Abstract.—Synthesis of sampling data from 1977 through 2001, including extensive mark–recapture data, provided a comprehensive and current picture of the status, population dynamics, and future prospects of the endangered Kootenai River white sturgeon *Acipenser transmontanus*. Natural recruitment was inconsistent in the 1960s, and with the additional impact of Libby Dam since the 1970s, the wild population now consists of an aging cohort of large, old fish. Jolly–Seber population estimates have declined from approximately 7,000 white sturgeon in the late 1970s to 760 fish in 2000. At the current mortality rate of 9% per year, fewer than 500 adults will remain by 2005 and fewer than 50 by 2030. At current growth and maturity rates, hatchery fish being released since 1992 should begin recruiting to the adult population around 2020. Population projections describe a significant bottleneck in spawner numbers as the wild population declines but hatchery fish have not yet matured. Only 113–203 wild females are projected to contribute to hatchery broodstock over the expected life span of the current population. With current levels of hatchery production, the population is projected to stabilize at about 3,000 adults—although numbers predicted by these population simulations are extremely sensitive to estimates of survival rate. The next generation is expected to be produced primarily from hatchery spawning of wild adults. Habitat restoration measures to improve survival and rearing conditions for the wild component are critical to recovery efforts in the long term; however, recovery measures should also include a balanced consideration of the short-term and long-term risks faced by the white sturgeon population. Use of increasing numbers of broodstock in the hatchery will reduce risks of genetic founder effects. Increasing numbers of juveniles produced per family in the hatchery will provide a hedge for uncertainty in broodstock availability as the population declines.

Although white sturgeon *Acipenser transmontanus* is typically an anadromous species, the Kootenai River (spelled Kootenay in Canada) of British Columbia, Canada, and Montana and Idaho, USA, currently contains a unique headwater population that has been isolated from the ocean and other Columbia River populations for about 10,000 years (Northcote 1973). Compared with other Columbia and Snake river white sturgeon populations, Kootenai River white sturgeon have less genetic diversity (Setter and Brannon 1992; Anders and Powell 2002), are active at cooler temperatures (Paragamian and Kruse 2001), and

spawn in different habitats (Paragamian et al. 2001).

Population assessments conducted around 1980 indicated that recruitment was inconsistent and in many years failed (Andrusak 1980; Partridge 1983); studies in 1989 confirmed that the population then consisted of a dwindling number of adults (Apperson and Anders 1991; Paragamian et al. 1996, 2001). Kootenai River white sturgeon were listed as endangered under the U.S. Endangered Species Act on September 6, 1994 (Duke et al. 1999; USFWS 1999). Decreases in white sturgeon have been concurrent with extensive habitat changes resulting from Kootenai Lake regulation, channel confinement, upstream flow regulation, and nutrient loading. Surface elevations of Kootenai Lake have been regulated since 1932 by Cora Linn Dam at the lake outlet (Duke et al.

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1999). Extensive diking throughout the lower Kootenai River from 1920 to 1950 isolated the river from the floodplain (Daley et al. 1981; Redwing Naturalists 1996). In 1972 the Kootenai Reservoir was created 40 km upstream from Kootenai Falls by construction of Libby Dam, which contributed to a further decline in white sturgeon. Unregulated spring flows before Libby Dam construction ranged from 1,700 to 2,800 m³/s (Apperson and Anders 1991). Peak flows after Libby Dam construction have generally ranged from 250 to 450 m³/s (Duke et al. 1999; Paragamian and Kruse 2001). Nutrient sump effects of Lake Kootenai were documented after an initial burst of reservoir productivity after completion of Libby Dam in 1972 (Woods 1982; Snyder and Minshall 1996; Anders et al. 2002; Paragamian 2002). In addition, nutrient-rich discharges from a phosphate fertilizer plant, changes in land use, and municipal sewage were significant before the mid-1960s. Corresponding changes in Kootenay Lake productivity from eutrophic to ultraoligotrophic have been concurrent with the collapse of many resident fish populations including kokanee *Oncorhynchus nerka* and burbot *Lota lota*. Recovery efforts for white sturgeon have included partial restoration of spring flows from upstream hydropower dams (Duke et al. 1999). Spawning and egg deposition have been observed in most years under current conditions, but the poor survival of eggs and larvae continues to preclude significant natural recruitment (Paragamian et al. 2001; Paragamian and Wakkinen 2002). A conservation hatchery program was initiated in 1990 as a stopgap measure to preserve the remaining population (Ireland et al. 2002a, 2002b). In this program, wild broodstock are spawned artificially and juveniles are reared for release at 1 or 2 years of age. Approximately 14,000 juveniles have been released in this program from 1992 through 2002 (S. C. Ireland, Kootenai Tribe of Idaho, unpublished data).

Accurate assessment of the status and population dynamics of Kootenai River white sturgeon is crucial for the preservation and recovery of these fish. Current numbers and survival rates of the wild component are necessary to determine the population trajectory and the estimated time remaining before the wild population becomes functionally extinct. Back-calculated year-class strength can help identify conditions suitable for successful recruitment. Expected numbers of mature wild spawners affect both the likelihood of natural spawning if suitable conditions can be restored and the prospects for capture of ripe fish

for spawning in the hatchery. Assessments of the wild population status and population dynamics also can help guide conservation hatchery efforts. Hatchery broodstock collection numbers and juvenile stocking rates have been based on hypothetical survival, growth, and maturation rates projected to produce the minimum effective population size necessary to preserve genetic integrity (Kincaid 1993).

Hatchery measures have been the subject of considerable debate with respect to whether current broodstock and release numbers are adequate to recover the population (Paragamian and Beamesderfer 2004). Our goal here was to provide a comprehensive and current picture of the status, population dynamics, and future prospects of the Kootenai River white sturgeon by analyzing population data from all Kootenai River and Kootenay Lake white sturgeon sampling efforts from 1977 through 2001. Our objectives were to determine population age composition and size (both abundance and biomass); quantify population dynamics, including rates of recruitment, survival, growth, and maturation; and project the population trajectory on the basis of this information, with and without hatchery releases. Where appropriate, we compared population parameters with estimates for other white sturgeon populations to provide a context for interpretation. This information should be vital to the future recovery planning of Kootenai River white sturgeon and might be useful as a template for other white sturgeon populations at risk.

Study Area

The Kootenai River originates in the Kootenay National Park, British Columbia, and flows through Montana and Idaho before joining the upper Columbia River in British Columbia (Figure 1). White sturgeon range from Kootenay Lake upstream 190 km to Kootenai Falls but are primarily found in the low-gradient reach between Bonners Ferry, Idaho, and the lake. Kootenay Lake is a large montaine natural lake (389 km² in surface area and 107 km long).

Methods

Fish sampling.—White sturgeon data are available for periodic but substantial sampling from 1977 through 2001 with setlines, angling, and gill nets (Andrusak 1980; Partridge 1983; Apperson and Anders 1990, 1991; Apperson 1992; Apperson and Wakkinen 1993; Marcuson 1994; Marcuson et al. 1995; Paragamian et al. 1995, 1997, 1999,

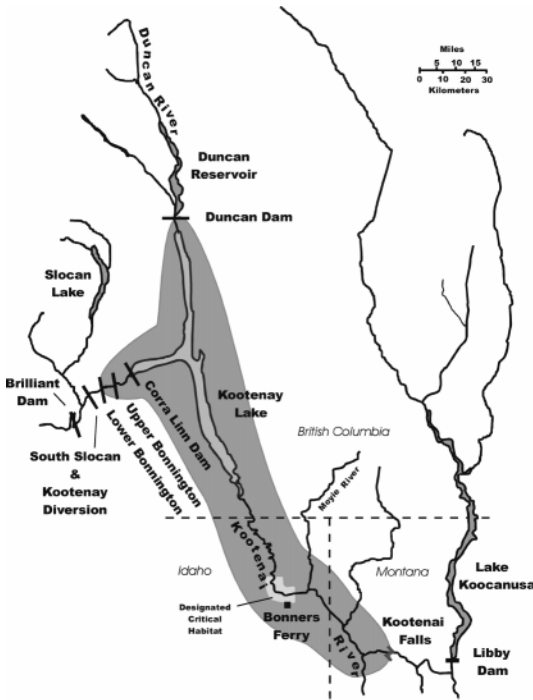


FIGURE 1.—Map of the Kootenai River, showing the current range of endangered wild Kootenai River white sturgeon.

2001a; RLL 1999). Similar gear was used in all sample periods although the effort allocated to each varied. During most years, sampling was concentrated in spring and summer in the U.S. portion of the Kootenai River downstream from Bonners Ferry but periodically included the Canadian portion of the river and Kootenay Lake.

Data collected from most fish included total length (TL), fork length (FL), weight, and the presence of tags or marks. Fish were marked with spaghetti tags from 1978 to 1983 and thereafter with passive integrated transponder (PIT) tags. Fish were also marked by removal of a lateral scute to identify recaptured fish that had lost their tag. These secondary marks indicated very low rates of tag loss over the course of the study, especially for PIT-tagged fish. Hatchery and wild fish were distinguished with PIT tags and scute marks. Only wild fish were included in analysis of sample data for this study. Sex and stage of maturation (Conte et al. 1988; Apperson and Anders 1991) were identified by surgical biopsies. Pectoral fin ray sections were collected from a subset of the sampled fish and used to estimate age. Percent year-class strength of the total catch was compared against

peak flow data provided by the U.S. Army Corps of Engineers, Seattle District.

Population parameters.—Length and age composition of the population were compared over time with frequency distributions and average values. Time intervals included three management periods (1977–1983, harvest fishery; 1989–1996, catch and release; and 1997–2001, postendangered species status). Estimated ages from fin rays were corrected for underestimation biases identified from mark–recapture studies data (Paragamian and Beamesderfer 2003). Corrections were based on age-specific biases that increased from 0 bias at age 0 to a maximum of 1.6 times the assigned age for fish age 25 and greater (smaller fish were assumed to be less subject to aging error than older fish were).

Abundance was estimated from multiple mark–recapture data by using an open Jolly–Seber model (Seber 1982; Pine et al. 2003) and POPAN-5 analysis software (Arnason et al. 1998a, 1998b). Release and recapture observations were paired and reformatted into an encounter history format. We fit a death-only model that assumed no births or new entries on basis of observations of an extended interval of little or no significant natural recruitment. Population biomass was estimated from abundance, period-specific length composition, and average length-specific weight.

Relative year-class strength was quantified based on age-frequency distributions. This analysis was limited to data from 1977 to 1983, where young fish were still present, because younger fish were more likely to provide an unbiased estimate of age (Paragamian et al. 1996; Paragamian and Beamesderfer 2003). Relative year-class strengths were back-calculated from observed age frequencies by assuming an estimated average annual survival rate of 85%. Approximate recent wild recruitment numbers were estimated on the basis of catch data from unmarked wild juveniles and of capture probabilities from juveniles reared in the hatchery and released into the Kootenai River (Ireland et al. 2002b).

Mortality rates were estimated from mark–recapture data by using MARK analysis software (White and Burnham 1999; Cooch and White 2001) and from age-frequency data by using the catch-curve method (Ricker 1975; Fabrizio et al. 1997). Annual capture probabilities and corresponding confidence intervals were derived concurrently with survival rate estimates by using the MARK analysis software and a recaptures-only model. Survival estimated with this model is ap-

parent survival (1-emigration-mortality). We assumed that emigration was a minor component because the Kootenai system is closed by dams on each end. MARK facilitated exploration of alternative pooling assumptions of survival rates and capture probabilities based on a parameter index matrix. Equal yearly survival rates were specified in the mark-recapture analyses within the pre-1989 and the 1989-present periods to obtain robust average estimates. Thus, both survival and population estimates were based on the Jolly-Seber model, albeit with slightly different formulations. Catch-curve analyses were stratified into time periods to minimize confounding effects of unstable age frequencies resulting from inconsistent or failed recruitment. Post-1988 rates in the absence of fishing can be construed to represent largely natural mortality. Mortality rates before complete fishery closures represent natural plus fishing mortality. Individual growth rates of wild fish were estimated from length at age and were described with von Bertalanffy functions (Ricker 1975; Paragamian and Beamesderfer 2003). Condition factor was described by using the relative weight (W_r) index (Murphy et al. 1991; Beamesderfer 1993) and exponential length-weight functions (Ricker 1975).

Maturation and sex were identified based on the presence of running sex products or surgical biopsy. Biopsies were made through a small ventral incision using standard methods reported for white sturgeon (Conte et al. 1988; Van Eenennaam and Doroshov 1988). Stage of gonadal maturation was visually classified on the basis of size, shape, and color. Maturation lengths were inferred from stage-frequency distributions and corresponding ages were based on average length-at-age curves. Sigmoid maturation curves (Beamesderfer et al. 1995) were fit to female length maturation distributions by nonlinear regression. Fits were based on the proportion of maturing (spawning next year) rather than the proportion of mature (spawning this year) fish because concentrated sampling effort near spawning areas resulted in disproportionate catches of ripe females. White sturgeon exhibit a 2-year egg maturation cycle (vitellogenesis), so next year's spawners can be distinguished by the presence of eggs in early developmental stages (Conte et al. 1988; Van Eenennaam and Doroshov 1988). The 2-year cycle means that mature and maturing females should be represented in equal proportions on average. We thus estimated the average population proportion of females spawning each year (after Beamesderfer et al. 1995) as

$$\begin{aligned} & \text{proportion maturing} \\ & \div [(2 \times \text{proportion maturing}) \\ & + \text{proportion not mature or maturing}]. \end{aligned}$$

Population trajectory.—Future white sturgeon population size, female spawner numbers, biomass, and size composition were projected with a simple age-structured population model based on current numbers and population parameters (Table 1). A simple spreadsheet model was developed specifically for this application. This model is similar in formulation to the MOCPOP model (Beamesderfer 1991) that has previously been applied to white sturgeon (Beamesderfer et al. 1995) and Gulf sturgeon (Pine et al. 2001) except that natural and hatchery fish numbers were tracked separately. The simulated period was begun in 1980, when population data were first available, and run for 100 years. Model population sizes were initialized for 1980 by calibration to the most recent population estimate (760 fish in year 2000) at the average annual survival rate estimated between 1980 and 2000. The model was initialized with actual hatchery releases for 1992 through 2002; for subsequent years, releases of 12,000 age-2 fish per year, the current hatchery production goals, were assumed (Ireland et al. 2002b). Forward simulations assumed minimal natural recruitment, which is equivalent to current levels.

Annual survival rates of adults and subadults were based on our estimates from mark-recapture data, except that rates before 1984 also included a presumed fishing mortality rate of 10.5%, estimated from the difference in total mortality before and after harvest was prohibited. Fishing mortality was applied to fish between 92 and 183 cm TL, consistent with fishing regulations in Idaho from 1979 to 1983. Juvenile mortality rates were based on estimates for hatchery fish reported by Ireland et al. (2002b). Hatchery fish were also assumed to have additional mortality during their first year as estimated by Ireland et al. (2002b). To account for changes in length/age composition, fish were categorized as either juveniles, subadults, or adults. Adults were identified as the age at which some females first matured, whereas juvenile and subadult groups were split at age 10.

Length at age was based on von Bertalanffy functions, modeling all fish of a given age to be average length. Individual fish weights and population biomass were derived from length-weight regressions. Sex ratio was assumed to be 50% because reliable sex data were not available. Length-

TABLE 1.—Equations, definitions, and values of variables and parameters used to project population trajectories. All values are derived from data presented in this paper.

Variable or parameter	Definition	Value
$N_{x,t,o}$	Age-specific number of fish in population in any year; $= (N_{x-1,t-1})(S_x)$	
x	Age	
t	Year	
o	Origin (wild or hatchery)	
$t = 1$	Initial year	1980
$N_{t,w}$	Initial wild population size	6,813
R_h	Annual hatchery recruitment	12,000
R_w	Annual wild recruitment	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	0.105
n_x	Natural mortality rate	
	<Age 11	0.100
	Age 11+	0.087
	First year after hatchery release	0.400
L_x	Length at age; $= L_\infty \cdot \{1 - \exp[-k(x - t_0)]\}$	
L_∞	Von Bertalanffy equation length at infinity	276
k	Von Bertalanffy equation slope parameter	0.0145
t_0	Von Bertalanffy equation intercept parameter	-3.12
W_x	Weight at age; $= (a_w)(L_x)^{b_w}$	
a_w	Length-weight equation coefficient	0.416
b_w	Length-weight equation exponent	3.12
pf	Proportion of the population that is female	0.50
ps_x	Proportion of the population of females of each age class that spawn in any year; $= 1 - [1/(1 + C_\infty \cdot \theta)]$ for $L_x \leq \mu$, $= 1 - \{1/[1 + C_\infty \cdot (1 - \theta)]\}$ for $L_x > \mu$	
C_∞	Maximum proportion of spawning females	0.333
θ	Cumulative normal distribution function dependent variable; $= 1/(2\pi)^{0.5} \cdot \exp[-(L_x - \mu)^2/\sigma^2] \sum_{i=1}^x b_i \{1 + p [(L_x - \mu)/\sigma]\}^{1-i}$	
μ	Mean length of females at sexual maturity	140
σ^2	Variance about mean length of females at sexual maturity	20
b_1, \dots, b_5	Constants	0.31938153, -0.356563782, 1.781477937, -1.821255978, 1.330274429
p	Constant	0.2316419

^a Exploited size range = 92–183 cm.

specific female maturation was based on our calculations of sigmoid maturation functions.

Future population sizes were compared with the critical population benchmarks associated with irreversible consequences in U.S. Endangered Species Act assessments. We used the benchmarks of 500 and 50 (Thompson 1991; McElhany et al. 2000; Rieman and Allendorf 2001). Genetic impacts accrue rapidly as the effective breeding population size declines to low levels (Soule 1980; Lande and Barrowclough 1987). Numbers less than 500 are reported to result in bottlenecks, which may rapidly reduce genetic diversity, and numbers less than 50 result in severe genetic impacts related to inbreeding (Thompson 1991; Rieman and Allendorf 2001). Loss of diversity and inbreeding depression associated with small effective population sizes may substantially reduce population fitness and productivity (McElhany et al. 2000). Small population sizes also can be sub-

ject to depensatory population processes (also known as Allee effects) that hasten the decline to extinction (Courchamp et al. 1999; Musick 1999; Gilpin and Soule 1986). Because of considerable uncertainty concerning small population risks, these benchmarks are best used as reference points for evaluating the effects of alternative recovery trajectories, not as hard criteria.

The expected contributions to the next white sturgeon generation were estimated from past numbers of broodstock collected and projected future collections by the hatchery. Projections were based on females, which appear to be more limiting than males in broodstock collection efforts to date. Projections included 23 females used from 1990 to 2000 and 6 females per year thereafter, consistent with current production goals and hatchery capacity. Numbers were referenced to female population size in 1990, when the hatchery began, and to number of females spawning per year.

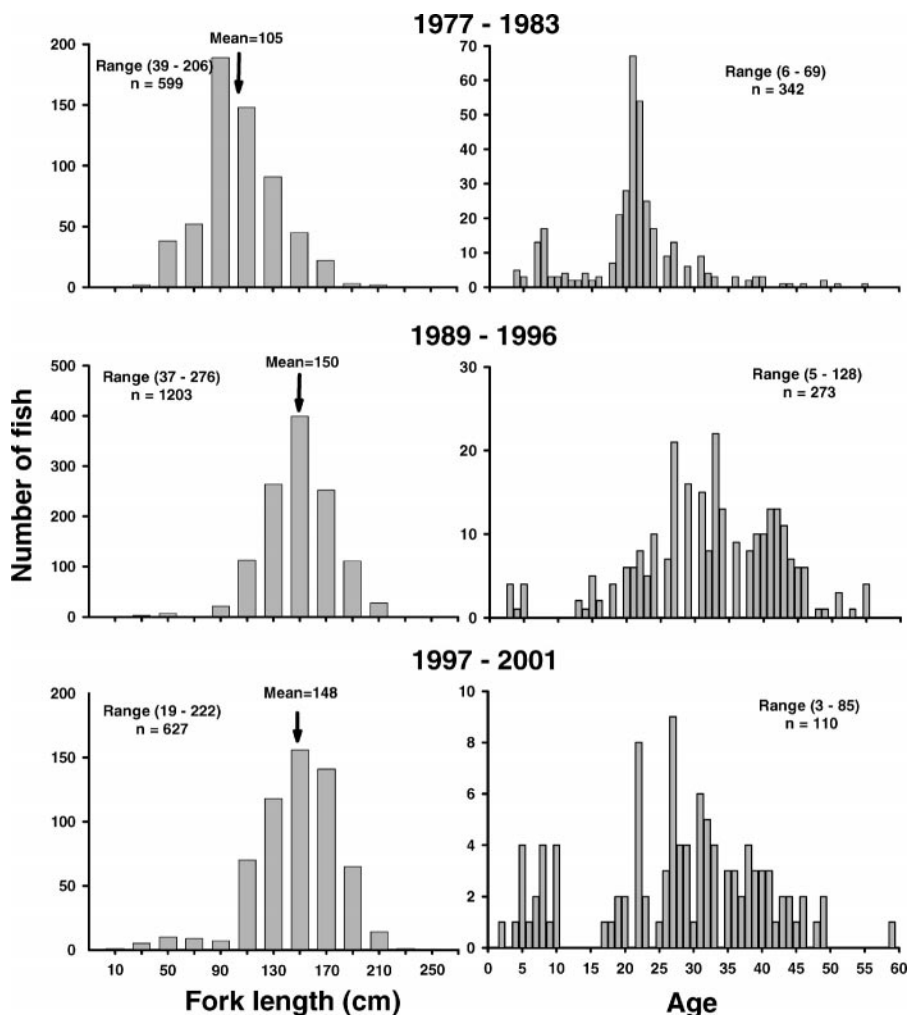


FIGURE 2.—Length and age frequency data of the Kootenai River white sturgeon population across three time periods from 1977 to 2001.

Results

Population Characterization

Length and age composition.—The wild Kootenai River white sturgeon population is currently dominated by large, old fish. Wild juveniles (<100 cm FL) virtually disappeared from length distributions after 1983 (Figure 2). Hatchery fish contributed 94% of the 659 juveniles that have been captured since hatchery fish were first released. The age composition of wild fish has shifted from a population dominated by fish of age 25 and younger to one comprising primarily fish older than 25 (Figure 2).

Abundance and biomass.—Mark-recapture data for wild fish were available for 22 of 25 years

between 1977 and 2001 (Figure 3). Annual catches ranged from 2 to 258 fish. Recaptures became a steadily increasing percentage of the catch, and most fish in the population have now been caught at least once. Capture probabilities ranged from less than 1% to 22%, reflecting substantial variations in sampling effort among years; over the past 8 years, probabilities have averaged 10–15% (Figure 3). Standard errors for annual capture probabilities generally ranged from 1% to 4%. Wild population size was estimated to be 760 fish in 2000, based on a Jolly–Seber model that assumed no significant wild recruitment. This population size is about half of the 1,470 estimated in 1996 and less than 10% of numbers estimated for the late

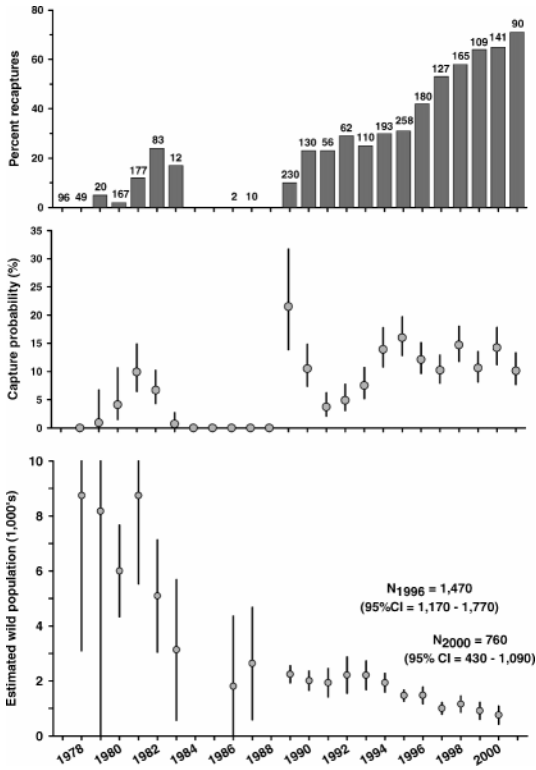


FIGURE 3.—Percent of the annual catch consisting of recaptures of previously tagged fish, estimated proportion of the population captured each year, and estimated abundance of wild white sturgeon, 1997–2001. Histogram labels state the total catch in a year, and error bars represent 95% confidence intervals (CIs).

1970s (Figure 3). Large numbers of recaptures and multiple recaptures from the aging cohort of long-lived fish provided for precise population estimates in recent years. Standard errors for population estimates decreased from a maximum of 53% for the 1979 population estimate to 33% for the 1999 estimate.

Recruitment.—Expansions of 1992–2001 annual catches from 0 to 11 wild fish per year suggest that annual recruitment has recently averaged approximately 10 fish per year. Consistent annual recruitment of large year-classes has not been observed since before 1960 (Figure 4). Historic year-class strengths appeared to decline over a 5–10-year period, following an apparent peak around 1950. Only one significantly large year-class (around 1974) has occurred in the last 40 years, as determined from high counts of age-6 fish in 1980 and age-7 fish in 1981.

Mortality.—The wild population is currently declining by about 9% per year according to esti-

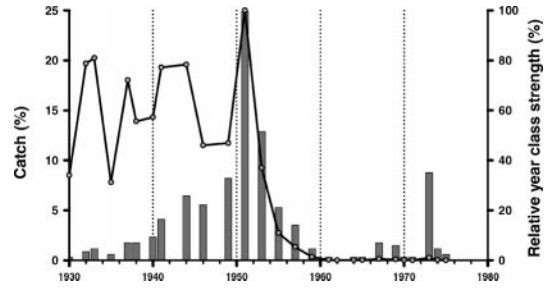


FIGURE 4.—Year-class frequency distribution (bars; left scale) and relative year-class strength (dots connected by lines; right scale) of Kootenai River white sturgeon captured from 1977 to 1983. Relative year-class strength was calculated on the basis of a hypothetical total annual mortality rate of 15%.

ated annual mortality rates. Average annual mortality rates estimated from mark–recapture data were 18.3% for 1977–1989 (95% confidence interval [CI], 16.0–21.1%) and 8.7% for 1989–2001 (95% CI, 6.8–10.9%). Mortality rates estimated from catch curves were 10.8% for 1977–1983 ($r^2 = 0.85$), 7.2% for 1989–1996 ($r^2 = 0.93$), and 5.6% for 1997–2001 ($r^2 = 0.84$). Both sets of estimates suggest that total annual mortality rates have decreased by approximately half over the past 25 years, which is concurrent with fishery closures. Discrepancies between mark–recapture and catch-curve results are consistent underestimations from catch curves biased by the decreasing trend in recruitment.

Growth and condition factor.—Average annual growth increments were 2.5 cm/year for fish 10–50 years old, based on von Bertalanffy curve fits to length-at-age data. Individual variation in length at age was great. The observed maximum size of 276 cm FL was substantially less than the theoretical maximum length (L_∞) of 331 cm identified by an unconstrained von Bertalanffy function. Estimated growth rates increased over time although differences were very small. Growth rate parameters (k) increased from 0.0128 in 1977–1983 (95% CI, 0.0126–0.0131) to 0.0156 in 1989–1996 (95% CI, 0.0153–0.0160) and to 0.0161 in 1997–2001 (95% CI, 0.0154–0.0168). The relative weight of wild white sturgeon has declined from a robust average of 100% in 1977–1983 ($n = 471$) to 92% in 1989–2001 ($n = 1,119$). Differences in relative weight between these time intervals were statistically significant ($P < 0.0001$), based on a nonparametric Wilcoxon two-sample test (SAS 2000). Changes in relative weight between these time periods were consistent across different sizes

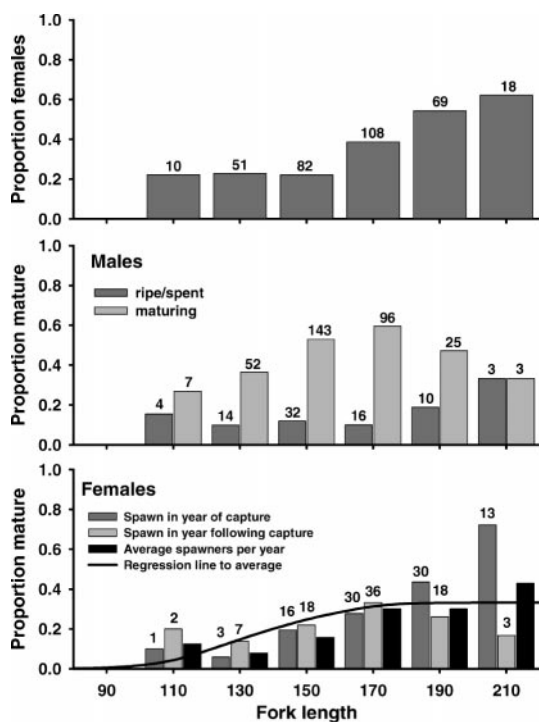


FIGURE 5.—Proportion by size-group of females in the sample (upper panel), ripe or spent and maturing males (middle panel), and mature females (lower panel) based on pooled Kootenai River sturgeon sample data from 1977 to 2001. Numbers above the histograms are the numbers observed. Regression lines for the average number of females maturing per year are based on sigmoid functions.

and hence did not appear to be an artifact of the changing size composition of the population. Corresponding length–weight exponent (a) and intercept (b) parameters were 3.34 and 1.65×10^6 in 1977–1983 and 3.12 and 4.16×10^{-6} in 1989–2001.

Maturation and sex.—The sex ratio of the sample was skewed toward males of 180 cm or less FL because males generally mature at smaller lengths and younger ages than females and because sampling is concentrated near spawning areas, where mature fish are more likely to be sampled than immature fish (Figure 5). Lengths of maturing and ripe/spent males were as small as 97 and 115 cm FL, respectively. The proportion of males that were maturing, ripe, or spent peaked at 170 cm FL (Figure 5). Thus, based on age–length curves, male maturation occurred between approximately 100 and 170 cm FL and between 28 and 65 years of age. Immature white sturgeon classified as males were reported at lengths from 105 to 218 cm. It is

unclear how many of these fish represent males that have not yet reached maturity, males that do not spawn every year, or males that may be senile or misidentified.

Females matured at between 110 and 210 cm FL (Figure 5). Corresponding ages were 30–100 years, based on the age–length curves. Concentrated sampling near prespawn staging and spawning sites to capture ripe fish for hatchery broodstock resulted in many more late-vitellogenic, ripe, and spent females than early vitellogenic females in the sample (Figure 5). The observed average female maturity of 31% at 180 cm FL or greater (corrected for sample site biases) was consistent with a physiological minimum 3-year spawning interval that includes the 2-year maturation cycle and one resting year. Thus, approximately one-third of the large, fully mature females would be expected to spawn each year. A lesser fraction of the smaller females would spawn in any year because some small females may not yet have matured and the spawning interval may possibly be greater in small females.

Multiple biopsies of individual fish observed in different years are consistent with the average 3–5-year spawning periodicities derived from maturation frequencies for the current size and age distribution of white sturgeon in the Kootenai River population. A total of 10 females were observed on two occasions in some stage of development from which spawning year could be inferred (Table 2). Observed intervals between spawnings ranged from 2 to 10 years but were generally 4 or 5 years. Assumed developmental periods of 18–24 months, on which the estimations of spawning years were based, were consistent with observations of three fish with late vitellogenic eggs at first capture and, on recapture in the next year, eggs from these fish were ripe, spent, or resorbed. Observed conditions of one other fish were inconsistent with assumed maturation cycles (Table 2). This fish was in early development during spring 1998 and in late development during spring 2 years later. Either the maturation cycle was protracted, or this fish immediately began the developmental cycle in the same year as presumed spawning (1999), or the stage of maturation was incorrectly assessed.

Population Simulations

With the almost complete failure of natural recruitment, the modeled white sturgeon population declined by almost 90%, from 6,800 fish in 1980 to 640 in 2002 (Figure 6). Initial population length and the declining trajectory were consistent with

TABLE 2.—Data on mature or maturing female white sturgeon biopsied in different years, with corresponding spawning intervals.

Fish	First observation				Second observation				Interval (years) ^a
	Date	FL (cm)	Stage	Spawning year	Date	FL (cm)	Stage	Spawning year	
1	Jun 9, 1989	219	Late	1990	Jun 8, 1990	211	Ripe	1990	
2	Jul 18, 1989	174	Late	1990	Sep 6, 1990	181	Spent	1990	
3	Oct 24, 1991	176	Late	1992	Jul 15, 1992	174	Resorbed	1992	
4	Mar 2, 1998	175	Early	1999	Apr 23, 2001	178	Late	2001	2
5	Jul 20, 1989	191	Late	1990	Apr 26, 1994	188	Ripe	1994	4
6	Mar 5, 1996	200	Ripe	1996	May 22, 2000	205	Ripe	2000	4
7	Aug 27, 1991	157	Late	1992	Apr 21, 1997	161	Ripe	1997	5
8	May 21, 1992	138	Late	1992	Mar 19, 1997	141	Ripe	1997	5
9	Jul 20, 1989	191	Late	1990	Mar 5, 1997	187	Attritic	1996	6
10	Jul 27, 1990	176	Early	1991	Mar 14, 2001	186	Ripe	2001	10

^a Fish may have spawned in the interval between known spawning instances without being observed.

estimates based on mark–recapture data for the same period (Figure 3). Current data indicate that the population declines by half every 7.4 years. Fewer than 500 adults from the existing wild population will remain by year 2005 and fewer than 50 adult fish by year 2030. Estimated total biomass has declined by about 75%, from 80 to 20 metric tons, from 1980 to present. Annual numbers of

female spawners have declined from 270 per year in 1980 to about 77 in 2002. Fewer than 30 females will be spawning annually after year 2015.

Significant numbers of hatchery fish released beginning in 1990 can be expected to begin recruiting to the adult population after year 2020 (Figure 6). With significant annual releases projected through the foreseeable future, the adult population will rapidly increase from 2020 to 2030, after which it is projected to stabilize at about 3,000 white sturgeon. This population size would be approximately five times the current adult population size and just under half the total number estimated in 1980. This prediction assumes of course that broodstock will continue to be available to sustain hatchery production during periods of very low spawner abundance between 2010 and 2030.

Extreme shifts in length and age structure occur as equilibrium is restored to the population. Adults made up more than 20% of total numbers from 1980 through 1995. From 1995 through 2015, the projected population consisted almost entirely of juvenile fish produced in the hatchery. Stable age and size composition will gradually be restored between 2015 and 2030 with adults, subadults, and juveniles contributing about 4, 31, and 65% of the population, respectively. Subadults will eventually contribute about 60% of the total white sturgeon biomass, whereas juvenile and adult shares will be 13% and 27%, respectively. At existing hatchery stocking rates, population biomass will eventually stabilize just over the level projected in 1980 when the population consisted primarily of adults.

Model simulations suggested that significant numbers of hatchery-origin female spawners will first appear around 2025 and steadily increase to an equilibrium number of about 50 fish per year.

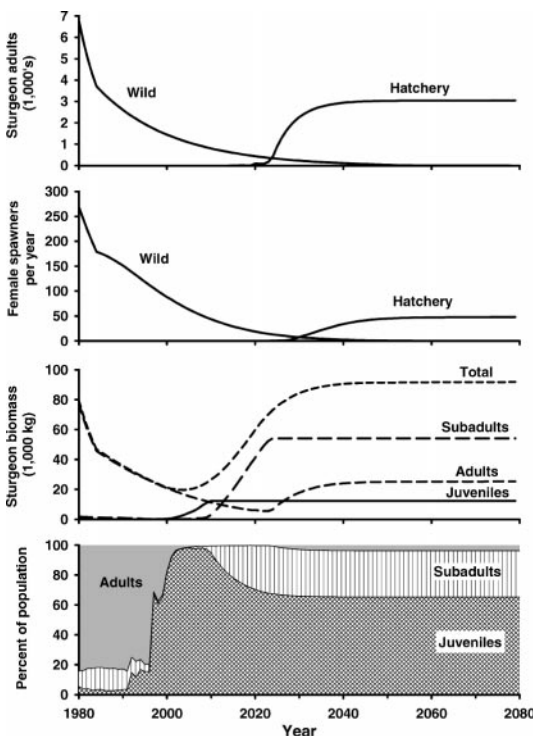


FIGURE 6.—Simulated population size, number of female spawners, total population biomass by life history stage, and size composition for Kootenai River white sturgeon from 1980 to 2080.

This number is similar to the projected number in 2008, two-thirds of the current number (77 in 2002) and about 20% of the back-calculated numbers for 1980. Equilibrium numbers are much less than historic numbers because the historic population included a much greater proportion of large, mature adults.

A total of 203 females would contribute to the hatchery broodstock through year 2030 if 6 ripe females can be collected per year. If females are no longer available after 2015, when the number of wild female spawners is projected to fall to fewer than 30 per year, a total of 113 female white sturgeon would have been used as broodstock. In either case, female broodstock numbers would represent only 10–20% of the adult female number in the population in 1990 when the hatchery program began.

Model predictions were extremely sensitive to estimates of annual survival rate. For instance, small changes (just $\pm 3\%$) in the annual survival of subadults and adults change the projected years for having fewer than 50 fish from 17 to 48 years (Figure 7). Projected numbers of hatchery adults at equilibrium change by approximately plus or minus 50%.

Discussion

Population Status

Extinction of wild white sturgeon in the Kootenai River is imminent. We estimated that only 630 adults remained in 2002 from a population 10 times that size just 20 years earlier. The population has now reached critically low numbers, where genetic and demographic risks become acute. Without immediate and substantive recovery measures to improve egg and larval survival, this population will not survive. Even immediate restoration of consistent conditions for recruitment may not be adequate to preserve the native diversity and production potential of this population.

Our population estimates, based on a Jolly–Seber population model, provide a more pessimistic view of current status than would be inferred from prior estimates. Various population sizes have been reported for the U.S. and Canadian portions of the Kootenai system, including 3,000–5,000 (Andrusak 1980), 1,148 (Partridge 1983), 880 (Apperson and Anders 1991), and 1,469 (Paragamian et al. 1996). These estimates appear to suggest that the population is relatively stable. However, this conclusion is an artifact of differences in models and assumptions used in obtaining the

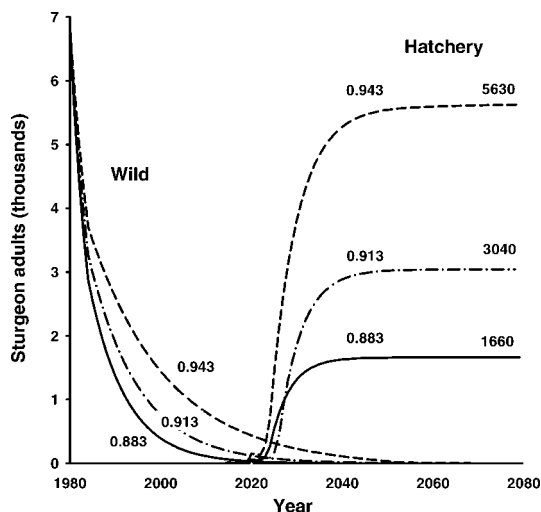


FIGURE 7.—Sensitivity of wild and hatchery-origin adult white sturgeon numbers to annual mortality rate in model projections for 1980–2080. Trajectories are plotted for the estimated annual mortality rate (0.913) and for hypothetical rates of the estimated rate 0.03. The values above the three rightmost curves are the numbers of hatchery fish over the long term.

various estimates. Our estimate of total numbers for 1978–1980 ($\sim 7,000$) is substantially larger than previous estimates for that time period. Earlier estimates, except for Paragamian et al. (1996), apparently underestimated total population size because only the Idaho river portion of the area used by the population was sampled. Use of a long-term data set and an open population model has provided a more accurate estimate of total numbers because the longer time period allows for a more complete mixing of marked and unmarked fish (Seber 1982). The Jolly–Seber model provides relatively unbiased estimates of population size despite temporary emigration (e.g., between Kootenai River and Kootenai Lake) as long as fish have a high probability of returning to the sample area and probabilities of capture are high (Zehfuss et al. 1999). The high individual recapture rates (averaging 27%) and frequent multiple recaptures (Paragamian and Beamesderfer 2003) suggest that most fish return to the sample area on multiple occasions throughout their long life span and have a high probability of being sampled during the 24-year sampling period. If this assumption is violated, then population estimates may be consistent underestimates, but they will continue to be indicative of the population trend.

Prospects for restoring natural recruitment through restoration of a more normal flow pattern

in spring remain uncertain. Flow measures implemented to date from Libby Dam have not been adequate to stimulate a year-class of substantial size and have fallen short of targets desired by many fish managers (B. Hallock, U.S. Fish and Wildlife Service, personal communication). Consistent historic recruitment appears to have coincided with wet years and high runoff conditions, which have been precluded by hydropower operations since completion of Libby Dam in 1972. In addition, spawning location of white sturgeon and in-river habitat changes post-Libby Dam construction appear to be important issues in recruitment (Paragamian et al. 2001, 2002). However, recruitment failures before Libby Dam construction suggest that early life history/recruitment may have also been affected by other habitat and ecosystem changes in the Kootenai system.

Population Dynamics

We estimate the current rate of population decline as approximately 9% per year, based on annual mortality rates in the absence of significant recruitment. Our estimates of annual mortality are similar to or less than rates reported for other white sturgeon populations but less than those used in early recovery planning. Natural mortality rates reported for other populations include 12% in the upper Columbia River (RLL 1994), 6–16% in the middle Snake River (Cochnauer 1983; Lukens 1985; Leppla and Chandler 1995, 1997), 4.2–9.0% in the lower Columbia River (Beamesderfer et al. 1995), and 5.0–16% in the Sacramento River (Kohlhorst 1980). Differences among reported estimates should be viewed with caution because the estimation methods varied, uncertainty in all reported natural mortality rates was high, and differences were relatively small. Initial hatchery release goals in recovery planning were based on an anticipated 20% annual mortality rate after age 4 (Kincaid 1993). Mortality rates of juvenile white sturgeon released from the hatchery were similarly less than expected rates (40% in year 1 versus 50% expected, 10% in subsequent years versus 30–40% expected; Kincaid 1983; Ireland et al. 2002b).

Reductions in the annual mortality rate of 5–10% during the past 20 years confirm that closure of this area to fishers has been a significant conservation measure. The extreme sensitivity of white sturgeon populations to fishing mortality is well documented (Rieman and Beamesderfer 1990; Boreman 1997). Increasingly restrictive possession, creel, size, and gear regulations were implemented in Idaho, Montana, and British Co-

lumbia between 1944 and the complete fishery closure in 1994 (USFWS 1999). Observed decreases in mortality rate were generally consistent with the limited data on harvest. A survey of about 86% of the white sturgeon fishing permit holders in Idaho from 1979 through 1981 showed a total catch of 675 white sturgeon and a harvest of 101 white sturgeon in the 3 years of angling (Partridge 1983). Andrusak (1980) estimated an annual fishery harvest of 100–120 white sturgeon in British Columbia waters before closure.

Kootenai River white sturgeon are among the slowest growing populations observed thus far. Growth rates are greater than those estimated for the Nechako River (Dixon 1986) but less than estimates for Sacramento–San Joaquin (Kohlhorst et al. 1980), lower Columbia (S. S. Hess, Oregon Department of Fish and Wildlife, unpublished report; Beamesderfer et al. 1995), upper Columbia (RLL 1994), Snake (Coon et al. 1977; Leppla et al. 2001; Lukens 1982), and lower Fraser rivers (Semakula and Larkin 1968). Individual growth rates actually increased slightly during the period when condition factors declined, contrary to our expectation that condition factor and growth rate would be positively correlated. No consistent differences were reported in age-specific incremental growth rates for periods before and after total river regulation by Libby Dam after 1977 (Young 2002).

Decreases in condition factor over time coincided with reduced productivity of the Kootenai River system. Relative weight of the white sturgeon decreased by approximately 10% over this interval. However, whether reduced system productivity may have reduced white sturgeon carrying capacity is unclear. Declining relative weights occurred in spite of reduced white sturgeon density, which should have diminished potential competition between fish if the population were food-limited.

Significant numbers of reproductive white sturgeon remain in the Kootenai population to take advantage of suitable spawning and rearing conditions if appropriate habitat can be identified and restored. Mature fish account for a large proportion of the female population. Spawning periodicity at full maturation (age 3–5 years) is similar to the 3 years reported for lower Columbia River populations (Beamesderfer et al. 1995) and close to the physiological minima of 2–3 years observed in California commercial aquaculture operations (M. A. H. Webb, Oregon State University, personal communication). The median size of female maturation (140 cm FL) was smaller than the medians

of 158–194 cm reported for lower Columbia River populations, perhaps reflecting the slow growth rates of the Kootenai River population. Beamesderfer et al. (1995) also observed a positive correlation between median length of female maturation and growth rate. No evidence of reproductive senescence or changes in gonad appearance was obvious in the reduced maturation frequency of large, old fish although sample numbers of these older fish were small.

Future Prospects

Current numbers and population dynamics confirm that time has not yet run out for the Kootenai River white sturgeon, but opportunities for effective intervention are rapidly dwindling. The long life span of white sturgeon provides an extended period in which to identify and implement effective but possibly contentious recovery measures. However, 40 years of this window of opportunity have now passed for Kootenai River white sturgeon. Consistent recruitment appears to have collapsed 20 years before the first systematic population surveys around 1980. Another 20 years then passed, during which the species was listed under the U.S. Endangered Species Act, a recovery plan was completed (Duke et al. 1999; USFWS 1999), a conservation hatchery program was developed (Ireland et al. 2002a, 2002b), and spring spawning flow measures were implemented (Paragamian and Kruse 2001; Paragamian et al. 2001; Paragamian and Wakkinen 2002).

The next 5–20 years will be a critical period in the preservation of Kootenai River white sturgeon. A bottleneck in spawner numbers will occur as the wild population declines yet the hatchery-reared fish released beginning in 1992 are not yet recruited to the spawning population. Even the immediate restoration of suitable habitat conditions for recruitment may not be sufficient to avoid adverse consequences of projected low population numbers.

Most likely, the next generation will be produced primarily or entirely by the conservation hatchery program. Postrelease assessments have found excellent condition, growth, and survival of hatchery juveniles, especially after an initial adjustment period (Ireland et al. 2002b). If fish managers had not initiated a conservation hatchery program as a contingency to habitat improvement measures, the current white sturgeon generation probably would have been the last.

Management Implications

The results of this assessment highlight an urgent need to update and revise the Recovery Plan (USFWS 1999) for the Kootenai population of white sturgeon. Habitat restoration measures to improve survival and rearing conditions for the wild component are critical to recovery efforts in the long term (Paragamian et al. 2001b; Paragamian et al. 2002), but recovery measures should also include a balanced consideration of the short-term and long-term risks faced by the white sturgeon population (Paragamian and Beamesderfer 2004). Efforts thus far have focused primarily on long-term population risks by attempting to restore natural production and limiting hatchery involvement to avoid inherent hatchery risks. Particular concerns have included ensuring a balanced contribution of hatchery broodstock to the next white sturgeon spawning generation (Kincaid 1993) and overseeding the available rearing habitat versus the risk of competition between hatchery and wild juveniles. However, risks to the current generation of the loss of genetic diversity, compensatory population processes, and impending spawning stock limitations may be much more important in the short term. Long-term considerations will be moot unless current recovery efforts are retooled to capture existing population diversity and to produce enough fish to ensure a next generation. Near-term risks can be reduced by increasing the numbers of broodstock used in the hatchery and the number of juveniles produced per family. Greater broodstock numbers will reduce genetic risks by maximizing the existing population diversity captured for the next generation. Projected broodstock numbers based on the current breeding plan and the wild population trajectory appear sufficient to reach a 50-parent inbreeding threshold but fall far short of a 500-parent diversity threshold. Larger release groups and equal family numbers will reduce demographic risks of small population size in the next generation. Expansion of current activities will also provide a hedge for uncertainty in broodstock availability as the population declines and uncertainty in future survival, growth, and maturation rates increases.

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