Evidence of density- and size-dependent mortality in hatchery-reared juvenile white sturgeon (*Acipenser transmontanus*) in the Kootenai River

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Abstract: We evaluated effects of stocking level and size-at-release on survival rates of hatchery-reared juvenile white sturgeon (*Acipenser transmontanus*) in the Kootenai River using Cormack–Jolly–Seber and related models implemented in Program MARK. A total of 119 768 marked and unmarked hatchery juveniles were released from 1992 to 2006, of which 2938 passive integrated transponder (PIT)-tagged fish were subsequently recaptured. Annual survival rates of marked groups ranged from 0.01 to 0.84 (mean = 0.45) during the first year at large, from 0.48 to 1.0 (mean = 0.84) in the second year, and averaged 1.0 during all subsequent years. First year survival rates declined substantially in recent years, particularly for small fish (<25 cm fork length). Approximately 59% of the variation in first year survival was explained by a negative relationship with estimated juvenile abundance (linear regression, $P < 0.01$). Length-at-release of individuals explained a substantial proportion of the within-year variation in survival during the first year at large. Our results provide strong evidence of density- and size-dependent mortality in hatchery-reared juvenile white sturgeon in the Kootenai River. Management actions that prioritize the release of fewer, larger-sized fish will likely improve first year survival rates and subsequent recruitment to the spawning-age population.

Résumé : Nous évaluons les effets de l'intensité de l'empoissonnement et de la taille à la libération sur les taux de survie de jeunes esturgeons blancs (*Acipenser transmontanus*) de pisciculture dans la Kootenai à l'aide du modèle Cormack–Jolly–Seber et de modèles apparentés utilisés dans le logiciel MARK. Un total de 119 768 jeunes de pisciculture marqués et non marqués ont été libérés de 1992 à 2006, dont 2 938 poissons porteurs d'étiquette PIT (à transpondeur intégré passif) ont été recapturés plus tard. Les taux de survie des groupes marqués variaient de 0,01–0,84 (moyenne = 0,45) durant la première année en liberté, de 0,48–1,0 (moyenne = 0,84) la seconde année et en moyenne de 1,0 durant toutes les années subséquentes. Les taux de survie durant la première année ont diminué considérablement au cours des dernières années, particulièrement chez les petits poissons (longueur à la fourche < 25 cm). Environ 59 % de la variation de la survie pendant la première année s'explique par une relation négative avec l'abondance estimée des jeunes (régression linéaire, $P < 0,01$). La longueur des individus à la libération explique une partie importante de la variation intra-annuelle dans la survie durant la première année de liberté. Nos résultats apportent de fortes indications de l'existence d'une mortalité reliée à la densité et à la taille chez les jeunes esturgeons blancs de pisciculture dans la Kootenai. Des activités de gestion qui favoriseraient la libération d'un nombre moins important de poissons de plus grande taille augmenteraient vraisemblablement les taux de survie pendant la première année et le recrutement subséquent dans la population en âge de frayer.

[Traduit par la Rédaction]

Introduction

A long individual life span has forestalled extinction of the Kootenai River white sturgeon (*Acipenser transmontanus*), listed in 1994 as endangered under the US Endangered Species Act (Duke et al. 1999). Natural recruitment began declining around 1960, and the last substantial year class was produced in the early 1970s (Andrusak 1980; Partridge 1983). Kootenai River white sturgeon continue to migrate upriver and spawn each year, but mortality of eggs and larvae is nearly absolute (Duke et al. 1999; Paragamian et al. 2001; Paragamian and Wakkinen 2002). The wild population now consists of a dwindling cohort of large, old fish (Paragamian et al. 2005).

Recruitment failure coincided with an accumulation of large-scale alterations of the Kootenai River system over the last 100 years, including extensive floodplain and watershed development, mainstem dam construction, reduced productivity, and shifts in the biological community across all trophic levels. Peak spring flows in the Kootenai River were greatly reduced following construction of Libby Dam

in 1972. Unregulated spring flows ranged from approximately 1700 to 2800 m³·s⁻¹ (Apperson and Anders 1991), while post-dam flows have ranged from only 250 to 450 m³·s⁻¹ (Paragamian and Kruse 2001). Beginning in the late 1800s, extensive floodplain development, including construction of levees, drainage ditches, and pumping stations, reclaimed substantial portions of historical floodplain habitat (Northcote 1973; Redwing Naturalists 1996). By 1990, approximately 90% of the historical wetlands and riparian habitats had been isolated from the river by levees (Soults and Anders 2003). In addition, the reservoir formed by Libby Dam currently acts as a nutrient sink, retaining considerable quantities of nutrients and organic material (Daley et al. 1981; Snyder and Minshall 1996). Although a variety of research and recovery measures have been implemented over the years, all efforts to date have failed to restore natural recruitment of Kootenai River white sturgeon or to identify a feasible strategy for restoring natural recruitment (Paragamian and Beamesderfer 2004).

It now appears that the next generation of Kootenai River white sturgeon will depend on a conservation aquaculture program initiated in 1990, without which the species would have been doomed to extinction (Paragamian and Beamesderfer 2004). Mature, wild fish are captured each year during the spawning migration, artificially spawned, and their progeny are reared in one of two hatcheries for 1 or 2 years before release into the wild (Ireland et al. 2002a; Kootenai Tribe of Idaho 2007). Survival of initial experimental hatchery releases was high, averaging 60% for the first year following release and 90% in subsequent years (Ireland et al. 2002b). Growth and condition were often poor within the first few years but increased in survivors that adapted to natural conditions. Large numbers of hatchery fish have been released in the interim.

Long-term prospects for sustaining any sturgeon population with a conservation aquaculture program remain highly uncertain. Depleted natural populations are being widely supplemented with hatcheries (Schram et al. 1999; Runstrom et al. 2002; Smith et al. 2002). However, hatcheries are considered to be poor substitutes for natural production and a conservation option of last resort for Kootenai River white sturgeon (Duke et al. 1999; Paragamian and Beamesderfer 2004). Important concerns include population bottlenecks or hatchery selectivity that may reduce genetic diversity and fitness, density-dependent mortality factors, and other ecological interactions related to overseeding the current habitat capacity (National Research Council 1996; Jager 2005; Drauch and Rhodes 2007).

The optimum number of broodstock and hatchery releases necessary to recover Kootenai River white sturgeon populations has been the subject of considerable debate (Paragamian and Beamesderfer 2004). Managers are faced with a difficult dilemma with respect to maximizing genetic diversity and recruitment to the spawning population while also avoiding overseeding of available rearing habitat. This study examines some of the critical uncertainties concerning the effects of increased hatchery production on survival of juvenile white sturgeon in the Kootenai River. Our objectives were to assess recent survival rates of hatchery-reared juvenile white sturgeon released into the Kootenai River and to examine the effects of size-at-release, environmental conditions, and increased stocking densities on survival.

Materials and methods

Study site

The Kootenai River contains a unique headwater population of white sturgeon that has been isolated from other populations in the Columbia and Snake rivers for some 10 000 years by natural falls at river kilometre (rkm) 24 (Northcote 1973). The Kootenai River is one of the largest tributaries to the Columbia River, draining approximately 35 490 km². Originating in British Columbia (BC), the river flows south into Montana where flows are impounded at Libby Dam (rkm 352) forming Koocanusa Reservoir (Fig. 1). From Libby Dam, the river flows west and then northwest into Idaho and then turns north into BC and Kootenay Lake near rkm 120. Kootenay Lake is a large, natural, oligotrophic lake, but the water level is now regulated by an outlet dam. Kootenai River white sturgeon range from Kootenay Lake upriver to Kootenai Falls, Montana (rkm 310), but are now found predominantly in the meandering, low-gradient reach downstream from Bonner's Ferry and in Kootenay Lake (Kootenai Tribe of Idaho 2007).

Fish sampling

Hatchery-reared juveniles were first released into the Kootenai River in 1992, and annual releases have occurred since 1997. Fish were reared for approximately 1–2 years at the Kootenai Tribal Sturgeon Hatchery in Bonners Ferry, Idaho, and at the Kootenay Trout and Sturgeon Hatchery in Ft. Steele, British Columbia. Releases were broadly distributed throughout the river, with release locations ranging from within Kootenay Lake (rkm 75–120) to sites as far upriver as Kootenai Falls (rkm 307). Prior to release, most hatchery-reared fish were measured (fork length and total length), weighed, and implanted with an individually numbered passive integrated transponder (PIT) tag. Fish were also marked by removal of lateral scutes to identify the fish's brood year in case of tag loss. More detailed information about the aquaculture program including brood stock collection and mating practices, fish health, size and numbers of river releases, sampling effort, and growth and condition is provided in Kootenai Tribe of Idaho (2007).

For analysis purposes, we grouped hatchery releases by year of release. Release year was defined as 1 March through 28 February, ensuring that all winter releases were included in the same year. For example, fish released in December 2005 and January 2006 were both defined as 2005 releases. Limited numbers of recaptures, particularly in recent years, precluded estimation of separate survival rates for fish grouped by release season or rearing facility.

Recapture data were provided by an annual juvenile white sturgeon monitoring program initiated in 1993 by the Kootenai Tribe of Idaho (KTOI), Idaho Department of Fish and Game (IDFG), and the British Columbia Ministry of Environment (MOE). Sinking multifilament gill nets with variable mesh size (1.0–6.3 cm) were fished between June and September at sites distributed from Kootenay Lake to the head of Kootenai Valley just upriver of the Kootenai Tribal Hatchery (rkm 77–236). Sampling locations were selected to represent a variety of available habitat types distributed throughout the river. Sampling effort varied considerably across years, with the total number of gill net hours ranging from a low of 298.4 in 1995 to a high of 890.6 in 2001.

Fig. 1. Range of white sturgeon (*Acipenser transmontanus*) in the Kootenai River Basin (shaded). Inset shows location in western Canada and USA.
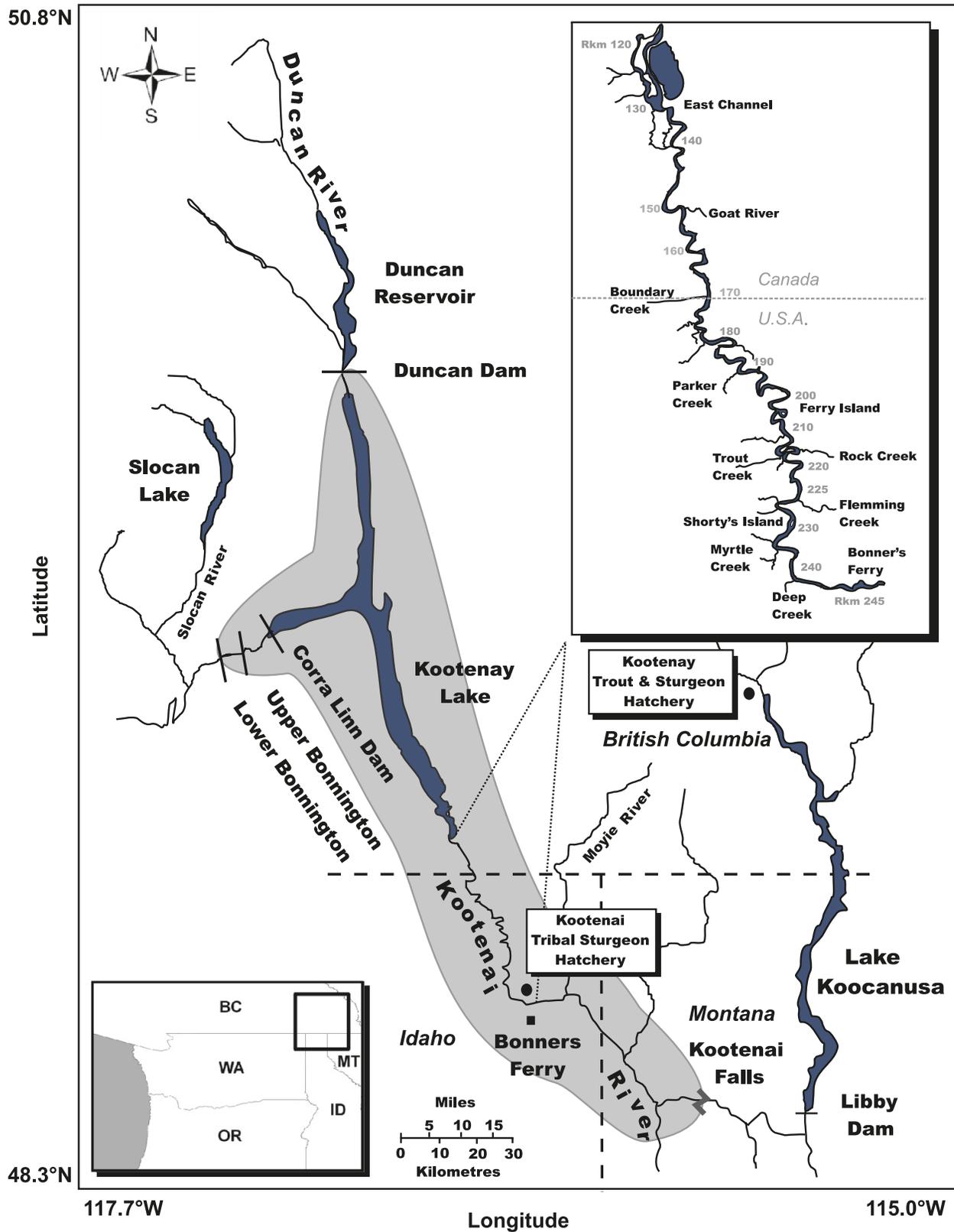
Table 1. Description of the nine noncovariate models (Models 1–9) and two length covariate models (Models 10–11) used to analyze capture–recapture data of juvenile white sturgeon (*Acipenser transmontanus*) released into the Kootenai River from 1992 to 2004.

Model	Model notation	Survival (φ)	Recapture (p)
1[a]	$\varphi(t)$, $p(t)$	Year-specific (t)	Year-specific
2	$\varphi(a2\text{-}c/c)$, $p(t)$	Two age classes (a; age-1 and age-2+); both constant (c) across years	Year-specific
3	$\varphi(a2\text{-}t/c)$, $p(t)$	Age-1 year-specific Age-2+ constant	Year-specific
4	$\varphi(a2\text{-}t/t)$, $p(t)$	Both ages year-specific	Year-specific
5	$\varphi(a3\text{-}t/c/c)$, $p(t)$	Three age classes (age-1, age-2, and age-3+); age-1 year-specific, age-2 and age-3+ constant	Year-specific
6	$\varphi(a3\text{-}t/t/c)$, $p(t)$	Age-1 and age-2 year specific, age-3+ constant	Year-specific
7	$\varphi(a3\text{-}t/t/t)$, $p(t)$	All three age classes year-specific	Year-specific
8	$\varphi(a3\text{-}t/t/c)$, $p(a2\text{-}t/t)$	Same as Model 6	Both ages year-specific
9[b]	$\varphi(a3\text{-}t/t/t)$, $p(a2\text{-}t/t)$	Same as Model 7	Both ages year-specific
10	$\varphi(a3\text{-}l + t/t/c)$, $p(t)$	Same as Model 6 but with a constant (additive) length covariate for age-1	Year-specific
11	$\varphi(a3\text{-}l \times t/t/c)$, $p(t)$	Same as Model 6 but with a year-specific (multiplicative) length covariate	Year-specific

[a]Standard Cormack–Jolly–Seber model.
[b]Global model (i.e., most parameterized).

Survival rates

Survival rates of juvenile white sturgeon were estimated for PIT-tagged juveniles released and recaptured in the Kootenai River. Fish released into Kootenay Lake were excluded from the analysis because there was limited sampling in the lake and few recaptures of lake-released fish. In addition, we removed 17 fish from the data set that were missing critical release information such as brood year and length-at-release. We also excluded recaptures that occurred in the same year that a fish was released or previously recaptured.

Annual apparent survival rates (φ) and recapture probabilities (p) were estimated using Cormack–Jolly–Seber (CJS) and related models implemented in Program MARK (White and Burnham 1999). Apparent survival (hereby referred to as survival) is distinguished from true survival in that apparent survival combines the probability of survival and the probability of not permanently emigrating out of the study area (i.e., $\varphi = 1$ – mortality – emigration), whereas true survival deals only with mortality. Thus, in open populations, substantial levels of permanent emigration will result in CJS survival estimates that are biased low compared with true survival. Although it is possible that some river-released juvenile white sturgeon may have permanently emigrated out of the study area (such as into Kootenay Lake), such behavior is assumed to be limited and is a topic of current research in the basin. In its most general form, the CJS model is parameterized to produce estimates of survival and recapture probability for each sampling period. Variations of the general CJS model, such as models that allow for group effects (e.g., age classes) or individual covariates (e.g., fish length) can be implemented in Program MARK to test specific hypotheses.

We had two objectives in our modeling of survival rates of hatchery-reared juvenile white sturgeon. The first objective was to determine the basic age and time structure that best captured variation in survival rates and recapture probabilities. From a biological perspective, we expect that sur-

vival rates of released juveniles may be initially low as juveniles transition to the river environment, especially during their first year at large (Ireland et al. 2002*b*; Golder Associates, Ltd. 2006). In subsequent years, survival rates should increase rapidly and stabilize as fish grow larger, approaching high annual survival rates typically observed for sturgeon populations (McCabe and Tracy 1994; Gross et al. 2002). Following this biological framework, we examined an initial set of (noncovariate) capture–recapture models to estimate baseline survival rates as described below. Our second objective was to test for possible influences of body size-at-release on survival rates of juveniles. A priori, we might expect that larger size-at-release could increase the chance of survival among newly released fish via competitive advantages or reduced risk of predation (Sogard 1997; Mohler et al. 2000; Sutton and Ney 2001). Thus, once the baseline model structure was determined, we then examined two additional models with length covariates to explicitly test for effects of fish size-at-release on survival rates.

The initial set consisted of nine models that built on those previously examined by Ireland et al. (2002*b*). The first model was the standard CJS model, which assumed year-specific survival rates ($\varphi(t)$) and recapture rates ($p(t)$) (Model 1; Table 1). The next three models included two age classes for survival, where the first age class represented the first year at large (age-1 fish), and the second age class represented all subsequent ages (age-2+ fish) (Models 2–4; Table 1). The underlying hypothesis for these age-structured models was that survival during the first year following release differed substantially from survival in all subsequent years, as found by Ireland et al. (2002*b*). These age-structured models assumed constant survival for both age classes (Model 2); year-specific survival for age-1 fish and constant survival for age-2+ fish (Model 3); and year-specific survival for both age classes (Model 4). The remaining models included three age classes for survival: the first year at large (age-1 fish), the second year at large (age-2 fish), and a third age class representing all subsequent

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Table 2. Number of hatchery-reared Kootenai River white sturgeon released from 1992 to 2006.

| Year | British Columbia hatchery | | | Kootenai Tribal Hatchery | | | Total |
	Tagged river releases	Tagged lake releases	Untagged river releases	Tagged river releases	Tagged lake releases	Untagged river releases	
1992	0	0	0	118	0	0	118
1993	0	0	0	0	0	0	0
1994	0	0	0	123	0	0	123
1995	0	0	0	0	0	0	0
1996	0	0	0	0	0	0	0
1997	0	0	0	1 959	0	0	1 959
1998	0	0	0	96	0	0	96
1999	0	0	0	334	0	0	334
2000	1 358	0	0	828	0	0	2 186
2001	3 237	0	0	2 777	0	0	6 014
2002	0	6 708	0	3 793	0	0	10 501
2003	0	7 579	0	8 382	0	0	15 961
2004	9 020	19	0	3 519	0	4 275	16 833
2005	1 238	0	4 240	0	0	32 560	38 038
2006	1 779	0	21 165	714	0	3 947	27 605
Total	16 632	14 306	25 405	22 643	0	40 782	119 768

ages (age-3+) (Models 5–9; Table 1). These models tested the hypothesis that survival rates differed during the first, second, and all subsequent years after release. The final two models assumed that recapture rates as well as survival rates were year-specific for both age classes (Models 8 and 9). These models allowed us to evaluate if recapture rates of age-1 fish differed from those of age 2+ fish, an effect that could result from size-selective gear effects. However, owing to limited statistical support for these models, investigation of additional models with three age classes for recapture probabilities was not warranted.

For models with year-specific survival rates for age-2 or older fish, we imposed parameter constraints to obtain viable estimates of age-1 survival for fish released in 1992. Because of limited sampling in 1993 and 1994, there were insufficient recaptures to estimate survival of 1992 releases in the first 2 years (no fish were released in 1993). Thus, where applicable, we set the survival rates for 1993 (age-2) and 1994 (age-3) to 1.0 (i.e., 100%), which allowed the age-1 survival rate for 1992 releases to be estimated using the observed recaptures in 1995. By fixing survival at 100% for 1993 and 1994, we assumed that all mortality between 1992 and 1994 occurred during the first year at large. Thus, the estimates for 1992 represent minimum estimates of age-1 survival. Also note that for CJS models, it is not possible to independently estimate survival and recapture probabilities for the last sampling period (Williams et al. 2002).

We selected the best fitting of the nine models using the quasi-Akaike information criterion (QAIC), which adjusts AIC by a variance inflation factor ($\hat{c}$) to account for potential overdispersion (Lebreton et al. 1992; Burnham and Anderson 2002). The QAIC model-selection criterion has been validated by simulation analyses (Anderson et al. 1994; Burnham et al. 1995) and is strongly recommended for capture–recapture studies (Lebreton et al. 1992; Burnham and Anderson 2002). Models were initially identified based on intuitive and biologically based structures. The strength

of competing biological hypotheses was interpreted using the QAIC results, which indicate the relative support of these biological hypotheses (i.e., alternative model structures) given the data at hand. Our analysis and discussion of trends in Kootenai River white sturgeon survival focused on results from the QAIC-selected best-fitting model in the absence of irregular and biologically or statistically unreasonable results for that model.

To compute $\hat{c}$, we assessed the goodness-of-fit of the global model (i.e., the most parameterized model; Model 9) using a parametric bootstrap method (Cooch and White 2007) and calculated $\hat{c}$ as the ratio of the global model deviance over the mean deviance from 500 bootstrap simulated deviances. As an additional measure of performance, we computed the QAIC weight for each model, which measures as the weight of evidence in favor of a given model as the best fitting in the model set (Burnham and Anderson 2002).

Effect of size-at-release

To examine the influence of fish length-at-release on survival rates, we added length covariates to the best-fitting model from the initial model set (Model 6). Because estimates for Model 6 and other competing models indicated substantial variation in age-1 survival rates but relatively high and consistent survival for older age classes, we only examined length effects for the first age class. We used fork length-at-release (cm) as the individual covariate instead of total length or weight because this measurement was most consistently available in the data set. The logit link function was used in Program MARK to transform relationships between length and survival to a linear scale.

Using Model 6 as a baseline structure, we examined two models that included length-at-release as a covariate influencing age-1 survival. We began by adding a constant (additive) length effect for age-1 survival rates (Model 10; Table 1). This model assumed that age-1 survival varied across years but that the slope of the length effect was con-

Table 3. Release and recapture information for passive integrated transponder (PIT)-tagged juvenile white sturgeon released by Kootenai hatchery programs (lake releases excluded), 1992–2005.

| | Releases | | | Recaptures | | | | | | | | | | | | | | | Individuals[a] | |
Year	Lower rkm	Upper rkm	Total	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	Total	Total	%
1992	204	243	117	1	0	14	26	9	9	17	8	3	8	7	7	0	2	111	63	54%
1994	204	310	120			12	16	12	9	9	13	10	10	2	4	0	5	102	56	47%
1997	241	245	1950						166	105	134	131	91	34	58	35	19	773	568	29%
1998	241	259	96							7	15	12	7	3	1	2	0	47	37	38%
1999	230	258	333								11	17	9	7	3	4	1	52	43	13%
2000	170	259	2186									140	60	63	64	57	39	423	363	17%
2001	170	245	6013										143	103	123	71	88	528	481	8%
2002	170	245	3793											51	46	28	31	156	151	4%
2003	170	301	8380												5	1	2	8	8	<1%
2004	144	307	12539													64	81	145	142	1%
2005	151	275	1238														5	5	5	<1%
Total			36765	1	0	26	42	21	184	138	181	313	328	270	311	262	273	2350	1917	19%

Note: Release numbers vary slightly from those reported in Table 2 because some individuals with missing release information (i.e., length-at-release or brood year) were removed from the data set prior to estimating survival rates.

[a]Number and percentage of individuals from a release group that were recaptured at least once.

Fig. 2. Fork length-at-release (cm) for passive integrated transponder (PIT)-tagged juvenile white sturgeon by release year, 1992–2005. Box plots show medians (horizontal lines), 25th–75th percentiles (boxes), 10th–90th percentiles (whiskers), and 5th–95th percentiles (dots).
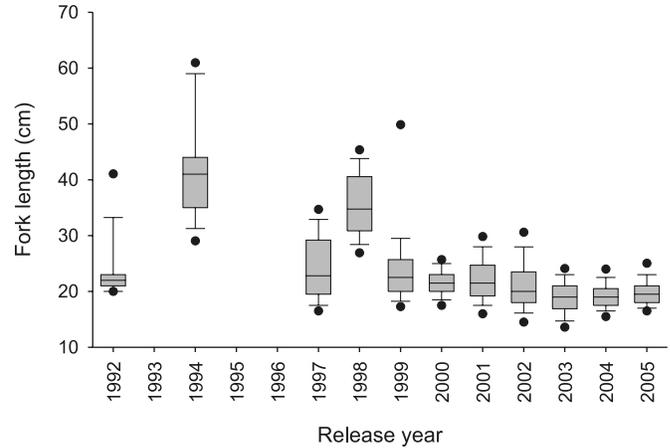
stant over time. The next model assumed a multiplicative relationship between length and time (Model 11); that is, the effect of length on age-1 survival varied across release years.

Again, we compared the models using QAIC to test the hypothesis that length-at-release influences survival of juvenile white sturgeon during their first year at large. Because no statistical procedure exists to evaluate goodness-of-fit of models that include individual covariates, we followed the recommended approach of using $\hat{c}$ as estimated for the global model excluding covariates (Model 9), as discussed above (Cooch and White 2007). We did not examine length effects for recapture probabilities of age-1 fish because there was little statistical support for age-class differences in recapture rates among noncovariate models.

To further examine the influence of fish length on survival, we compared size-at-release distributions for fish that were never recaptured with those for fish that were recaptured at least once. For each annual release group, we tested for differences in mean length-at-release between fish that were recaptured and not recaptured using a Wilcoxon rank sum test. We used this nonparametric test because size-at-release distributions were often non-normal.

Effect of environmental conditions and fish abundance

We used linear regression to evaluate relationships between age-1 survival rates and annual measures of environmental conditions and fish abundance by release year. Environmental variables included maximum annual river discharge, average annual river discharge, and average daily maximum temperature in August. The question was whether survival patterns were related to periodic floods or temperature extremes. Data on river discharge and temperature in the Kootenai River at Porthill, Idaho, were obtained from the US Geological Survey (USGS), National Water Information System (water.usgs.gov/). River discharge was summarized by release year (1 March – 28 February). Maximum daily river temperatures in each year were averaged for the month of August to correspond with the period when temperatures were warmest and most likely to affect juvenile

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Table 4. Comparisons of the 11 capture–recapture models (Table 1) fit to juvenile white sturgeon released in the Kootenai River from 1992 to 2004.

Model	Model notation	Parameters	QAIC	Noncovariate models		All models	
				ΔQAIC	QAIC weights	ΔQAIC	QAIC weights
1	$\varphi(t)$, $p(t)$	26	18 395.3	766.7	0.000	1 012.1	0.000
2	$\varphi(a2\text{-}c/c)$, $p(t)$	15	18 194.4	565.8	0.000	811.3	0.000
3	$\varphi(a2\text{-}t/c)$, $p(t)$	24	17 630.7	2.1	0.210	247.6	0.000
4	$\varphi(a2\text{-}t/t)$, $p(t)$	34	17 643.0	14.4	0.000	259.8	0.000
5	$\varphi(a3\text{-}t/c/c)$, $p(t)$	25	17 631.2	2.6	0.168	248.0	0.000
6	$\varphi(a3\text{-}t/t/c)$, $p(t)$	33	17 628.6	**0.0**	**0.611**	245.4	0.000
7	$\varphi(a3\text{-}t/t/t)$, $p(t)$	44	17 644.8	16.2	0.000	261.6	0.000
8	$\varphi(a3\text{-}t/t/c)$, $p(a2\text{-}t/t)$	42	17 636.7	8.1	0.010	253.6	0.000
9	$\varphi(a3\text{-}t/t/t)$, $p(a2\text{-}t/t)$	53	17 654.5	25.9	0.000	271.3	0.000
10	$\varphi(a3\text{-}l + t/t/c)$, $p(t)$	34	17 422.4	—	—	39.3	0.000
11	$\varphi(a3\text{-}l \times t/t/c)$, $p(t)$	43	17 383.2	—	—	**0.0**	**1.000**

Note: Values of quasi-Akaike information criterion (QAIC) for all noncovariate models (Models 1–9) and length covariate models (Models 10–11) were computed using the overdispersion parameter ($\hat{c}$ = 1.15) estimated for the global noncovariate model (Model 9). The QAIC results of the best-fitting noncovariate and covariate models are noted in bold.

Table 5. Estimates of survival rate and recapture probability (95% confidence intervals in parentheses) for the best-fitting noncovariate model (Model 6) and length covariate model (Model 11) for juvenile white sturgeon released into the Kootenai River from 1992 to 2004.

Year	Model 6			Model 11	
	Recapture probability	Age-1 survival	Age-2 survival	Age-1 survival	Age-2 survival
1992	—	0.70 (0.57, 0.86)	—	0.75 (0.57, 0.87)	—
1993	0.01 (0.00, 0.06)	—	Set to 1.0	—	Set to 1.0
1994	—	0.61 (0.48, 0.81)	—	0.64 (0.36, 0.85)	—
1995	0.17 (0.11, 0.24)	—	1.00 (1.00, 1.00)	—	1.00 (1.00, 1.00)
1996	0.27 (0.20, 0.36)	—	—	—	—
1997	0.14 (0.08, 0.20)	0.73 (0.60, 0.91)	—	0.63 (0.49, 0.75)	—
1998	0.12 (0.09, 0.15)	0.84 (0.57, 1.00)	0.63 (0.50, 0.79)	0.45 (0.03, 0.95)	0.66 (0.52, 0.79)
1999	0.12 (0.10, 0.15)	0.30 (0.21, 0.42)	0.89 (0.54, 1.00)	0.26 (0.17, 0.36)	0.93 (0.56, 1.00)
2000	0.15 (0.12, 0.17)	0.49 (0.43, 0.60)	1.00 (0.71, 1.00)	0.46 (0.39, 0.53)	1.00 (1.00, 1.00)
2001	0.14 (0.12, 0.16)	0.35 (0.30, 0.40)	1.00 (1.00, 1.00)	0.23 (0.19, 0.27)	1.00 (1.00, 1.00)
2002	0.07 (0.06, 0.09)	0.28 (0.21, 0.39)	1.00 (1.00, 1.00)	0.21 (0.15, 0.30)	1.00 (1.00, 1.00)
2003	0.05 (0.04, 0.06)	0.01 (0.00, 0.02)	0.76 (0.52, 1.00)	0.01 (0.00, 0.03)	0.76 (0.42, 0.93)
2004	0.06 (0.05, 0.07)	0.16 (0.12, 0.20)	0.47 (0.09, 1.00)	0.17 (0.14, 0.22)	0.48 (0.05, 0.94)
2005	0.04 (0.03, 0.04)	—	—	—	—

Note: Age-1 survival estimates for Model 11 were based on average-sized juvenile white sturgeon (mean fork length = 20 cm, standard deviation = 5 cm). Recapture probabilities and age-3+ survival estimates for Model 11 were identical to those for Model 6.

white sturgeon behavior and survival. Temperature data at Porthill was unavailable for 1997 and 2002. To supplement missing data for 2002, we used daily maximum temperatures collected at the Kootenai Tribal Sturgeon Hatchery. A comparison of August temperatures at the two locations across 3 years with overlapping data indicated that temperatures were very similar, with Porthill data averaging 0.2 °C cooler.

As an annual measure of Kootenai River white sturgeon abundance, we summed the total number of new releases (excluding lake releases) and the estimated number of fish that survived from previous years. The latter was estimated using the annual survival rates derived from the best-fitting noncovariate model (Model 6). We used age-1 survival estimates from both Model 6 and the best-fitting covariate model (Model 11) as dependent variables in regressions with total abundance and environmental variables. The latter comparison was used to test whether the decline in age-1

survival was related to total abundance or other environmental factors after removing the effect of size-at-release. Assumptions of the linear regressions were tested using graphical methods, the Shapiro–Wilk test for normality, and the Durbin–Watson test for autocorrelation.

Results

A total of 119 768 hatchery-reared juveniles were released between 1992 and 2006 (Table 2). These included 39 275 PIT-tagged fish released in the river, 14 306 released into Kootenay Lake, and 66 187 fish released without PIT tags. Excluding lake releases, unmarked fish, and individuals with missing release information, the number of PIT-tagged releases from 1992 to 2005 totalled 36 765 (Table 3). Initial releases were relatively small but increased substantially following development of rearing facilities at the BC hatchery

Fig. 3. Relationships between fork length-at-release (cm) and age-1 survival as estimated from the best-fitting covariate model (Model 11). No fish were released in 1993, 1995, and 1996.
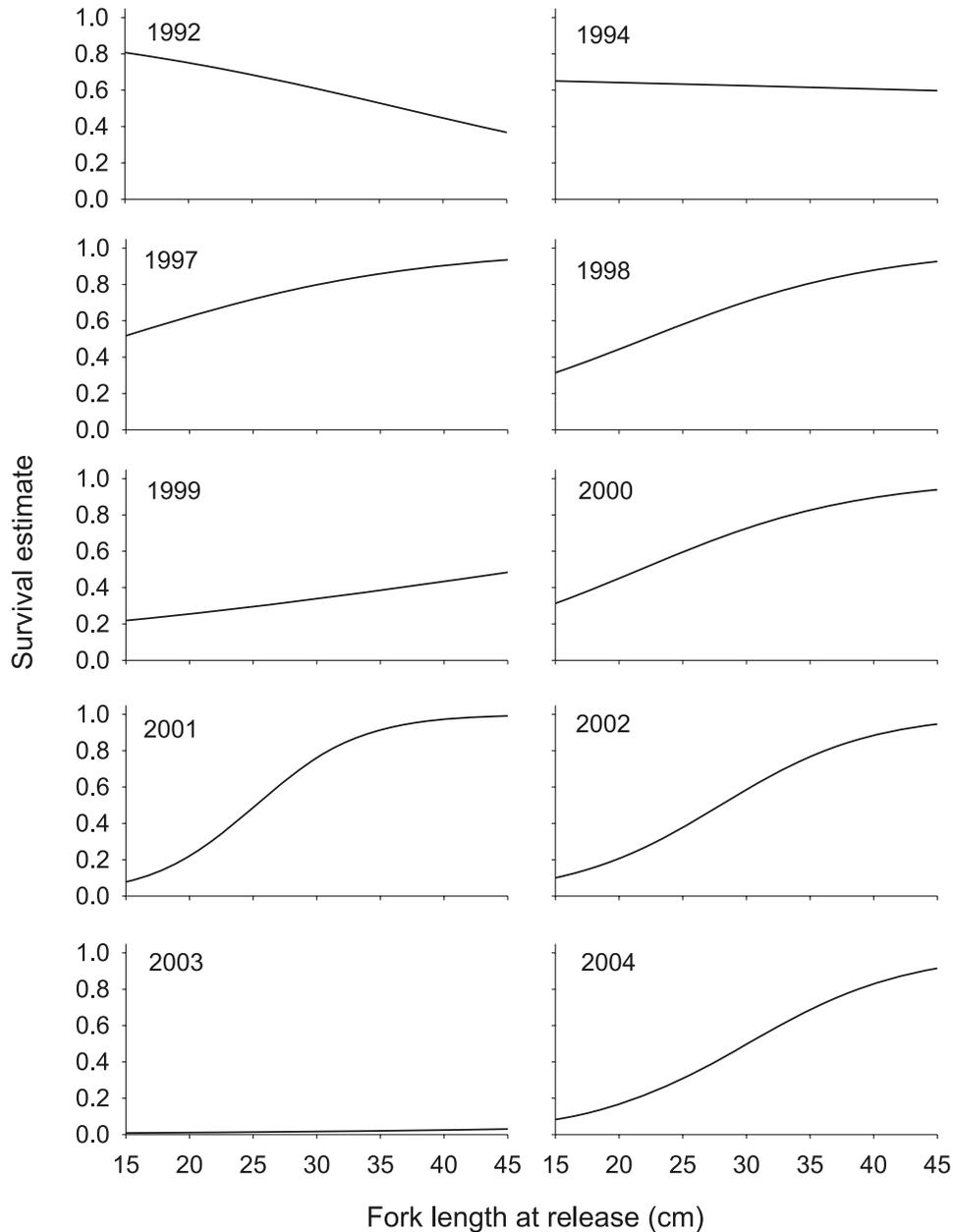
and upgrades to the Kootenai Tribal Hatchery in 1998 and 1999. Historically, individual fish size-at-release varied widely, ranging from 7 to 64 cm (mean = 20 cm; standard deviation, SD = 4 cm). More recently, smaller fish were released to maximize hatchery production (Fig. 2).

A total of 2938 PIT-tagged juveniles were recaptured between 1992 through 2006. Recaptures totaled 2350 after removing within-year recaptures and a small number of untraceable fish (Table 3).

Survival rates

Fits of the noncovariate capture–recapture models (Models 1–9) provided strong evidence of both age-specific and year-specific differences in survival rates of juvenile white sturgeon in the Kootenai River. The best-fitting model based on QAIC was Model 6 (Table 4), which specified year-specific survival rates for the first two age classes (age-1 and age-2), constant survival rates for the third age class (age-3+), but no age structure for recapture probabilities (Table 1). As model complexity increased, by far the largest improvement in fit (i.e., reduction in QAIC) resulted from the addition of year-specific survival rates for age-1 fish (Table 4). For example, ΔQAIC declined from 565.8 for Model 2 to 2.1 for Model 3. In contrast, the addition of year-specific survival for age-2 fish resulted in only a slight improvement in model fit (Model 6, ΔQAIC = 0). Model 5, which assumed constant survival across years for age-2 fish, was also a strong competing model (ΔQAIC = 2.6). In addition, there was little evidence that survival rates of age-3+ fish varied across years (Model 7, ΔQAIC = 16.2). Collec-

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tively, these results indicate (*i*) very strong empirical support that age-1 survival rates were distinctly time varying; (*ii*) comparatively weak evidence that age-2 survival rates either differed from older age classes or were distinctly time varying; and (*iii*) moderate support that survival rates of age-3+ fish were essentially constant across years.

Parameter estimates for the best model (Model 6) indicated that age-1 survival rates declined markedly over time, ranging from a high of 0.84 in release year 1998 to only 0.01 in 2003 (mean = 0.45) (Table 5). Survival estimates for age-2 fish were generally higher and less variable, ranging from 0.48 to 1.0 (mean = 0.84) (Table 5). In contrast, age-3+ survival was estimated to be 1.0 (95% confidence interval, CI = (0.97, 1.00)) across all years. Clearly, a survival rate of 1.0 (i.e., 100%) for age-3+ fish is unrealistically high. Nevertheless, this result suggests that age-3+ survival was consistently high across years but was statistically indistinguishable from 1.0 because of limited data and sampling error.

Survival estimates for age-1 fish were reasonably robust to assumptions regarding age structure. Across years, estimates for Model 6 were similar to, and highly correlated with, those for the top two competing models ($r = 0.97$ for Model 3 with no age-2 class; $r = 0.97$ for Model 5 with constant survival for age-2 fish), with absolute differences in age-1 survival estimates averaging less than 0.05 in both cases. The most obvious difference in age-1 survival estimates occurred for release year 1997, where survival was estimated to be 0.73 for Model 6 compared with 0.54 and 0.56 for Models 3 and 5, respectively.

Finally, there was little empirical support that recapture rates of age-1 fish differed substantially from those of older fish (Model 6 versus Model 8, ΔQAIC = 8.1; Table 4). For Model 8, estimates of recapture rates of age-1 fish were 26% lower on average than those for age-2+ fish, which is consistent with the hypothesis that young juveniles may be less vulnerable to recapture because of size-selective gear effects. However, there was considerable overlap among year-specific confidence intervals for the recaptures rates of each age group, and overall, little statistical support for such differences (ΔQAIC = 8.1). Importantly, age-1 survival estimates for Model 8 were again similar to those for Model 6 ($r = 0.97$; average absolute difference = 0.05).

Effect of size-at-release

The addition of length covariates to Model 6 greatly improved the model fit, suggesting that age-1 survival rates were strongly influenced by the length-at-release of individual fish. The best-fitting length covariate model based on QAIC was Model 11 (Table 4). This model incorporated a year-specific length effect for age-1 survival, indicating that the functional form (slope) of the length effect varied across years. Indeed, parameter estimates for Model 11 depicted considerable variation across years in the relationship between length and age-1 survival rates (Fig. 3). The influence of length is reflected by estimated slopes between length and logit(survival) (Fig. 4). Although slope estimates were imprecise, the direction of the length effect was consistently positive beginning with the 1997 release year (Figs. 3 and 4). This positive effect of fish length on first year survival

Fig. 4. Slope estimates (Model 11) for the effect of fork length-at-release (cm) on logit(survival) of age-1 fish for release years 1992–2004. Error bars represent approximate 95% confidence intervals. Values greater than zero (above broken line) indicate a positive effect of length on survival.
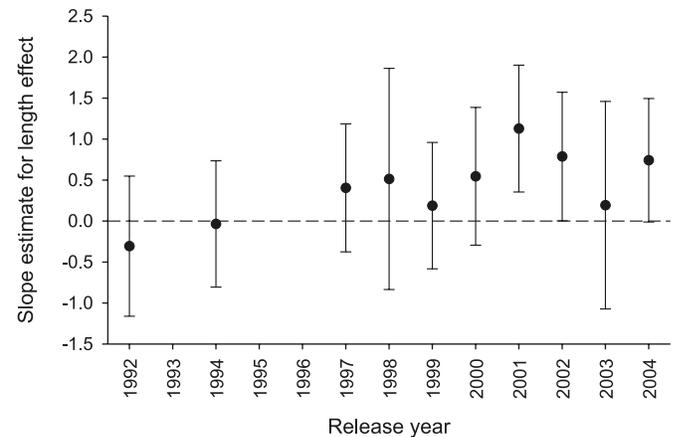
tended to increase over time and was highest for 2001 releases.

Annual estimates of age-1 survival for Model 11 are reported in terms of the average-sized fish across release years (mean = 20 cm, SD = 5 cm) (Table 5). These estimates were similar to the baseline survival estimates provided by Model 6 and showed a steady decline across years from a high a 0.75 in 1992 to a low of 0.01 in 2003 (mean = 0.38). The most notable difference between age-1 survival estimates was for 1998 releases (0.84 for Model 6 and 0.45 for Model 11). The estimated survival rate for 1998 was lower under Model 11 (the length covariate model) because this estimate was for an average-sized fish across years (20 cm), whereas the actual average length of 1998 releases was considerably greater (36 cm) (Fig. 2). In general, however, the similar declining patterns in age-1 survival estimates for Models 6 and 11 suggest that while length-at-release had important effects on survival, particularly in recent years, other factors were largely responsible for the declining trend in first year survival rates.

Comparisons of length-at-release distributions between fish that were recaptured and not recaptured generally corroborated the results from the length covariate models. That is, fish released at a larger size were more likely to survive and be recaptured for all releases since 1997 (Table 6). Mean length-at-release was significantly higher for fish that were recaptured versus not recaptured in five out of eight comparisons since 1997 (Wilcoxon test: $P < 0.05$). The largest positive differences in mean length (recaptured minus not recaptured) occurred for fish released in 2001 (difference = 2.5 cm) and 2002 (5.6 cm) (Fig. 5).
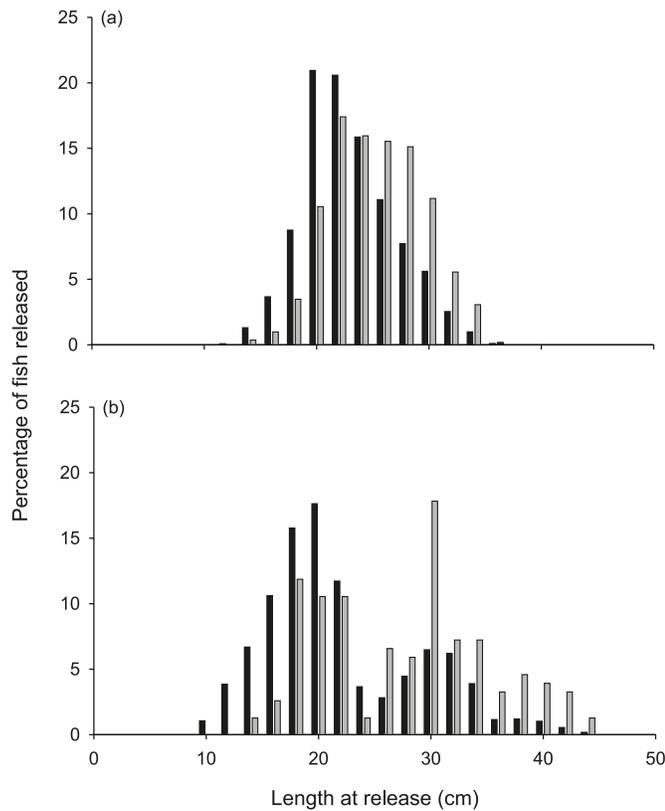
Effect of environmental conditions and fish abundance

Between 1992 and 2005, median annual river discharge in the Kootenai River at Porthill, Idaho, ranged from a low of 199 $m^3 \cdot s^{-1}$ in 2001 to a high of 561 $m^3 \cdot s^{-1}$ in 1996 (Fig. 6a). Relatively high flood events occurred in 1996 and 1997, with peak discharges exceeding 1500 $m^3 \cdot s^{-1}$ in both years. Median daily maximum stream temperatures during August ranged from 15.5 to 20.5 °C across years (median all years =

Table 6. Summary of Wilcoxon rank sum tests for comparisons between length-at-release distributions for juvenile sturgeon released but not recaptured and those recaptured.

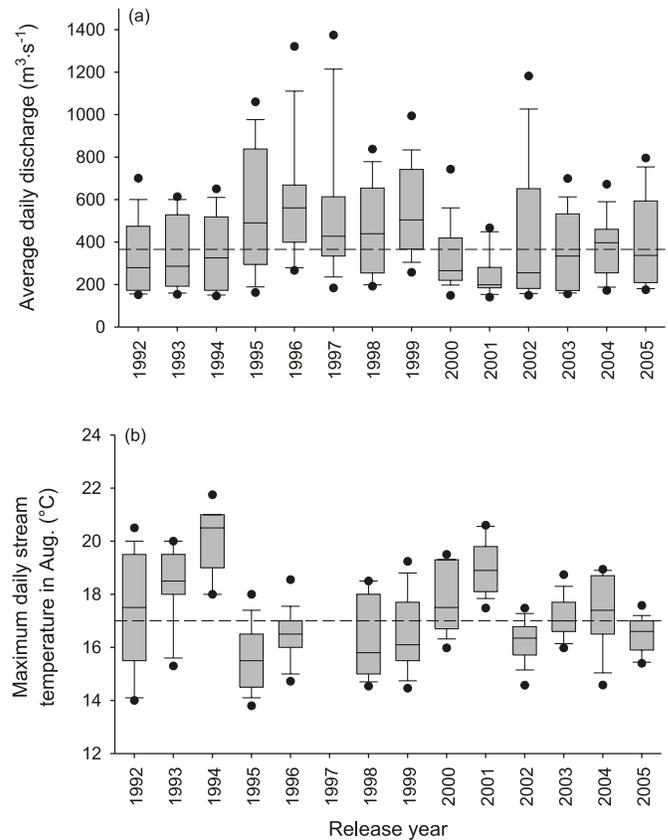| Release year	Mean fork length (cm)			Wilcoxon test		
	Not recaptured	Recaptured	Difference	df	W	P value
1992	24.6	23.2	–1.4	115	–0.3	0.755
1994	41.8	41.2	–0.6	118	2.2	0.030
1997	23.9	25.3	1.4	1 948	–4.3	<0.001
1998	35.2	36.6	1.4	94	–1.3	0.209
1999	24.2	27.1	2.9	331	–0.4	0.664
2000	21.4	21.9	0.5	2 184	–2.5	0.013
2001	21.9	24.4	2.5	6 011	–12.8	<0.001
2002	21.0	26.6	5.6	3 791	–8.8	<0.001
2003	18.6	19.3	0.6	8 378	–0.5	0.625
2004	19.1	20.3	1.1	12 537	–4.1	<0.001

Note: Difference refers to the difference between means (recapture – release); df refers to degrees of freedom.

Fig. 5. Distributions of length-at-release for juvenile sturgeon not recaptured (black bars) and recaptured (grey bars) for example release years (*a*) 2001 and (*b*) 2002.

Fig. 6. Distributions of (*a*) average daily discharge ($m^3 \cdot s^{-1}$) and (*b*) maximum daily river temperatures (°C) during August in the Kootenai River near Porthill, Idaho, for release years 1992–2005. Box plots show medians (horizontal lines), 25th–75th percentiles (boxes), 10th–90th percentiles (whiskers), and 5th–95th percentiles (dots). The broken horizontal line represents the median discharge across all years. Temperature data was unavailable for 1997.

17.0 °C) (Fig. 6*b*), with the warmest temperatures occurring in 1994 and 2001.

No significant relationships were observed between estimates of age-1 survival rate (Model 6 and Model 11; Table 5) and annual averages of environmental conditions (discharge, maximum discharge, and maximum daily temperatures) (linear regression: $P > 0.05$). These factors explained little of the annual variation in age-1 survival rates, with R^2 values ranging from 0.02 to 0.04.

In contrast, there was clear association between estimates of age-1 survival and fish abundance. Recent declines in

survival coincided with increases in both hatchery releases and estimates of age-2+ abundance (Fig. 7*a*). Abundances of age-2+ fish, which were estimated via survival estimates from Model 6, increased steadily from 82 fish in 1993 to 7897 fish in 2005. A linear regression of total juvenile abundance versus age-1 survival estimated from the best-fitting

Fig. 7. Estimated abundance (total releases + residual population) of hatchery-reared juvenile white sturgeon compared with (*a*) age-1 survival rates and (*b*) age-2 survival rates for release years 1992–2005. New releases, residual population, and survival rates are denoted by open bars, solid bars, and circles, respectively. Survival estimates were derived from the best-fitting noncovariate (Model 6).
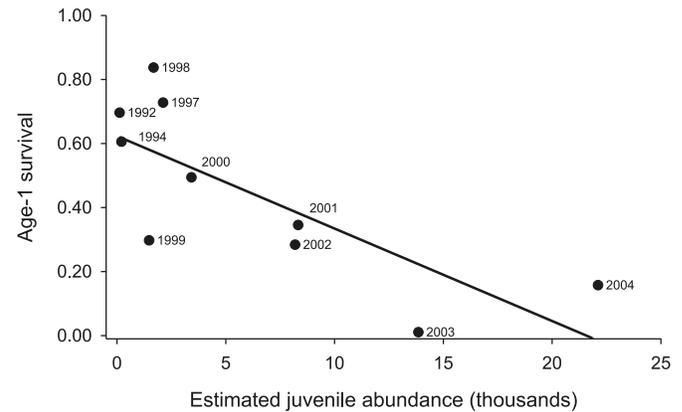

Fig. 8. Relationship between annual estimates of juvenile sturgeon abundance and age-1 survival rates. Survival estimates were derived from the best-fitting noncovariate model (Model 6).
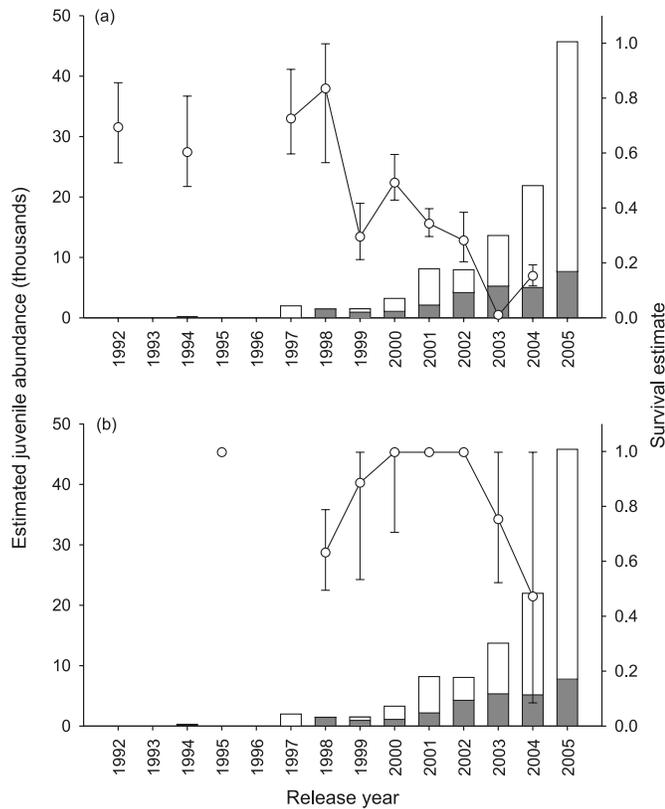
noncovariate model (Model 6) explained 59% of the variation in age-1 survival rates (Fig. 8; *P* = 0.01). Similarly, age-1 survival rates estimated using the best fitting covariate model (Model 11) were also negatively related to total juvenile abundance (R^2 = 0.56, *P* = 0.01). There was little evidence of a relationship between juvenile abundance and age-2 survival estimates (Fig. 7*b*).

Discussion

Survival of hatchery-reared juvenile white sturgeon declined in the first year following release into the Kootenai River in an apparent response to the cumulative effects of size- and density-dependent factors since the first hatchery releases in 1992. Prior to 1999, first year survival following release was relatively high, averaging 72%, and was not strongly related to fish size. First year survival of more recent releases declined to just 1%–49% per year (mean = 27%), accompanied by lower survival among the smaller fish within most release groups. In contrast, survival of age-2 fish did not exhibit a consistent trend over time, with estimates ranging from 48% to 100% (mean = 84%). After their second year in the wild, survival remained high (close to 100%) throughout the study period.

Poor first year survival of juvenile white sturgeon coincided with hatchery practices to release greater numbers of

small fish beginning in 2002. Hatchery production capacity is limited by juvenile rearing space. Releasing smaller, younger fish allowed the hatchery to produce more juveniles by avoiding seasonal space limitations caused by extended rearing of multiple overlapping brood years. The decision to release more and smaller fish was precipitated by projected demographic bottlenecks in wild abundance (Paragamian et al. 2005) and high rates of survival observed among initial release groups (Ireland et al. 2002*b*). It appears that this decision did not produce the expected demographic benefit because of declines in survival of smaller fish concurrent with increased production.

Our results suggest that density-dependent factors may be limiting survival of hatchery-reared juvenile white sturgeon in the Kootenai River. The decline in first year survival rates of the small white sturgeon in recent release groups coincided with increasing annual release numbers and increasing abundance of juvenile white sturgeon from previous releases. In contrast, there was little evidence to suggest that annual variation in environmental conditions such as discharge and river temperature substantially influenced survival of hatchery-reared sturgeon. This is the first reported evidence for density-dependent population dynamic processes in North American sturgeon of which we are aware. Density-dependent mortality appears to be concentrated among smaller juveniles (e.g., <25 cm in fork length) during their first year after release. Larger, older juveniles do not currently appear subject to the same limiting factors.

Collectively, these results appear to support a combined effect of both size-at-release and release number on survival of Kootenai River white sturgeon during their first year at large. Recent management decisions to release greater numbers of hatchery fish coincided with a reduction in average size-at-release, potentially confounding any distinct effects of density- and size-related mortality. Yet our findings provide evidence in support of both processes. Capture–recapture models that included a length covariate were heavily favored over the other models in terms of QAIC, suggesting strong empirical support for an effect of length-at-release on first year survival rates. In addition, for a fixed length-at-release of 20 cm (i.e., after accounting for annual differences in mean length-at-release), age-1 survival estimates still showed a strong declining trend in re-

cent years (Model 11) and a significant negative relationship with juvenile abundance ($R^2 = 0.56$, $P = 0.01$), indicating that much of the variation in first year survival was driven by other factors such as stocking densities or unknown environmental conditions. Thus, although the relative impacts of stocking density and size-at-release on first year survival remain uncertain, we contend that both factors should be considered carefully in future management and monitoring strategies.

The biological mechanisms driving the apparent density-related declines in first year survival of Kootenai River white sturgeon are unknown but might include competition or predation. Recent stocking levels of small sturgeon may have exceeded the current rearing capacity of the Kootenai River for this life stage. White sturgeon are also highly piscivorous, and the larger individuals from previous releases might be cannibalizing the smaller fish from more recent releases. Productivity of the Kootenai River has declined from historic levels, and food limitations are a real possibility. Lake Koocanusa, formed by construction of Libby Dam in 1972, is a nutrient sink, trapping nearly 63% of available nitrates and 25% of the phosphates destined for the lower Kootenai River (Woods 1982; Snyder and Minshall 1996). A recent energy budget developed for the Kootenai River indicated that autotrophic and detrital energy inputs were insufficient to sustain the estimated fish biomass downstream of Libby Dam (Snyder and Minshall 2005). In addition, estimated growth rates and condition factors of hatchery-reared juvenile white sturgeon in the Kootenai River were generally lower than averages for other populations (Ireland et al. 2002*b*).

Density-dependent rearing limitations among small juvenile white sturgeon in the Kootenai River may represent a critical second recruitment bottleneck. Other research has identified a severe bottleneck at the egg incubation stage (Paragamian and Wakkinen 2002). Significant numbers of fish are observed to spawn each year, and viability of embryos has been confirmed, but most spawning currently occurs over an unstable sand and silt substrate that is not conducive to survival (Paragamian et al. 2001; Anders et al. 2002; Kock et al. 2006). A density-related rearing limitation for young juveniles (e.g., age-1 fish) would be a second limiting life stage. Although this potential limitation was identified using hatchery fish, it is possible that a similar problem contributed to the historical decline in wild recruitment in the absence of hatchery fish. This second bottleneck would clearly compound the difficulty of restoring substantial natural recruitment. This finding highlights the potential utility of hatchery fish as surrogates for providing critical empirical information on survival bottlenecks and habitat limitations on natural production. However, competition with large numbers of hatchery fish could also reduce survival of wild sturgeon and complicate evaluations of other recovery measures.

The results from this study have important implications for the strategic goals of the aquaculture conservation program, recovery of white sturgeon in the Kootenai River, and other sturgeon populations at risk. Continued releases of large numbers of small-sized fish may severely limit survival of juvenile white sturgeon during the first year following release. Given the high estimated survival rates for age-2+ fish, management actions that prioritize the release of fewer, larger-sized fish will likely improve first year survival rates and subsequent recruitment to the spawning-age population. We recommend that (*i*) stocking numbers should be based on habitat suitability, expected survival, and available habitat; (*ii*) releases of hatchery white sturgeon should be contingent on abundance of wild white sturgeon of a similar year class as determined through research monitoring and evaluation; and (*iii*) a total hatchery population goal be developed based on stocking numbers, survival rates, and expected hatchery contribution to the total white sturgeon population. Consistent with an adaptive management strategy, the hatchery program has already implemented strategies to increase body size and reduce numbers of releases as suggested from this study.

While conservation aquaculture is a vital component to successful restoration of white sturgeon in the Kootenai River, it is only one aspect of an integrated ecosystem restoration program designed to address limiting factors for reproduction and recruitment. A variety of other actions have been implemented to improve conditions for recruitment in the wild, including flow and temperature management, river and tributary habitat restoration, nutrient augmentation, and re-establishment of native fish populations. Whether these efforts and the Kootenai hatchery program can effectively propagate white sturgeon through the next generation will depend on the ability of managers to anticipate, avoid, and adapt to new problems while pioneering a conservation recovery strategy with very limited room for error.

Acknowledgements

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