Fisheries Management
and Ecology

Fisheries Management and Ecology, 2011

White sturgeon spawning and discharge augmentation

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Abstract Observed spawning events of endangered Kootenai River white sturgeon, *Acipenser transmontanus* (Richardson), during 1994–2002 were examined to evaluate the effects of discharge from Libby Dam on spawning. Discharge from Libby Dam was manipulated in most years to provide enhanced flows (hereafter, augmented discharge) for white sturgeon spawning. The annual onset of spawning appeared independent of augmented discharge because initial spawning occurred prior to augmented discharge in 4 of 6 years. Spawning began 2–11 days after the highest river discharge in 4 of 9 years. Linear regression analysis indicated the onset of spawning was positively related to mean daily discharge from the dam but not mean daily temperature, 1-day change in discharge (Δ discharge) or 3-day Δ discharge. Logistic regression analysis suggested the probability of a spawning event was influenced by Julian date, mean daily water temperature, mean daily discharge and the 7-day Δ discharge, but the predictive indices were small. Minor fluctuations in temperature and discharge characteristics had little additional predictive benefit for spawning after the river reached spawning thresholds. The highest probability of spawning (0.48) was for the temperature interval 9.5–9.9 °C, and 93% of the estimated spawning events occurred above 8 °C. Sixty percent of the estimated spawning events occurred at discharges ≥600 $m^3 s^{-1}$, which comprised 45% of the range of discharge values.

KEYWORDS: *Acipenser transmontanus*, endangered species, discharge management, Kootenai River, Libby Dam.

Introduction

In Idaho, USA, all white sturgeon, *Acipenser transmontanus* (Richardson), populations have been affected by habitat and hydrologic changes because of hydroelectric and flood control dams that limit spawning and recruitment (Cochnauer *et al.* 1985; Lepla & Chandler 1997; Paragamian *et al.* 2001). Perhaps the most affected white sturgeon population in Idaho is that of the Kootenai River (Paragamian *et al.* 2005). Libby Dam in Montana, USA, was completed in 1972 by the US Army Corps of Engineers, became fully operational by 1974 and created Koocanusa Reservoir on the Kootenai River (Fig. 1). Soon after the operation of Libby Dam commenced the Kootenai River white sturgeon population downstream of Kootenai Falls in Idaho and British Columbia, Canada, was thought to have become recruitment limited (Partridge 1983; Apperson & Anders 1990). Although other anthropogenic factors may have had some effect on the decline of white sturgeon (Anders *et al.* 2002), dam operations had the most profound effect because it altered habitat. These effects were both physical and chemical. After Libby Dam became operational, the river temperature was about 1 °C cooler in the summer and 4 °C warmer in winter (Partridge 1983), and declining phosphorus decreased productivity (Woods 1982; Snyder & Minshall 1995). Pre-dam discharges during the white sturgeon spawning period ranged from about 1416 to 2832 $m^3 s^{-1}$. Peak discharges after Libby Dam was built generally were 250–450 $m^3 s^{-1}$, which almost eliminated the spring freshet and reduced sediment transport. Sediment transport reduction resulted in the loss of suitable incubation habitat for white sturgeon eggs by the accumulation of sand and fine sediment on cobbles and gravels at most spawning locations (Barton *et al.* 2006; Paragamian *et al.* 2009). The failed white sturgeon recruitment was attributed to egg suffocation resulting from accretion of fine sediments (Paragamian *et al.* 2009). As little as 5 mm of sediment can suffocate a white sturgeon egg (Kock *et al.* 2006).

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 doi: 10.1111/j.1365-2400.2011.00785.x

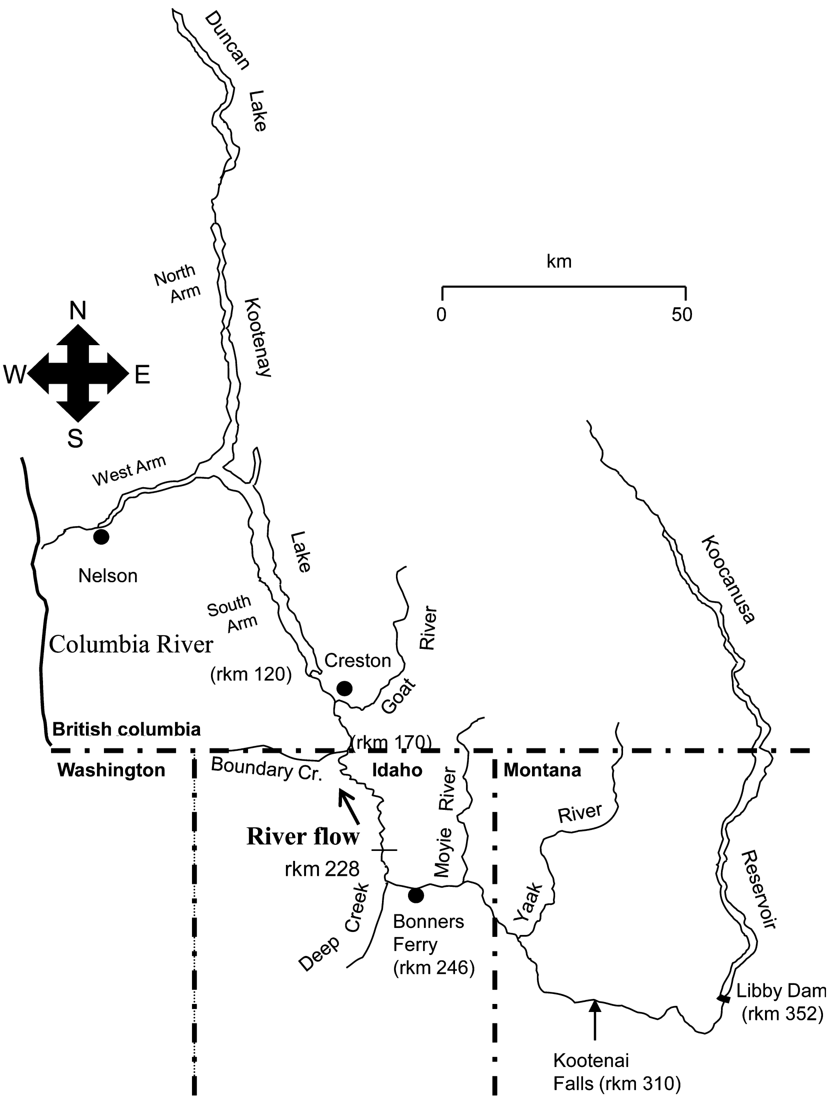

Figure 1. Location of the Kootenai River, Kootenay Lake, Koocanusa Reservoir, Libby Dam, Bonners Ferry, the Columbia River and important points. The river distances are kilometres from the northernmost reach of Kootenay Lake.

The US Fish and Wildlife Service listed the Kootenai River white sturgeon population as endangered under the US Endangered Species Act on 6 September, 1994 (USFWS (U. S. Fish and Wildlife Service) 1994; Duke *et al.* 1999). An international, multi-agency recovery team wrote a recovery plan in 1999; one of the main recovery measures was to restore migration and spawning and rearing habitat by maintaining discharges greater than the 113 $m^3 s^{-1}$ discharge (USFWS (U. S. Fish and Wildlife Service) 1999; Duke *et al.* 1999). The additional volume of water to be released from Libby Dam each spring specifically for white sturgeon spawning (discharge above normal dam operations before listing the white sturgeon as endangered; hereafter, augmented discharge) was determined by an inflow forecast for Koocanusa Reservoir for the April to August period. The augmented discharge was determined using a six-tier protocol [USFWS (U. S. Fish and Wildlife Service) 1999; Duke *et al.* 1999]. Tier 1 prescribed the release of no additional water for white sturgeon spawning in the driest years when the April to August water-inflow forecast was < 1.2 billion m^3. Tier 2 prescribed a release of 2.1 billion m^3 of water when the April to August inflow forecast was 5.9–7.4 billion m^3. Tier 6 prescribed a release of 7.8 billion m^3 of water when the April to August inflow forecast was 9.9 billion m^3 or greater.

Initial studies suggested discharges for white sturgeon spawning in the Kootenai River should be > 630 $m^3 s^{-1}$ and ideally > 1200 $m^3 s^{-1}$ (Paragamian

& Wakkinen 2002). Spawning usually occurred when river temperature was at least 8 °C, and most spawning occurred when water temperatures were 9.5–12.5 °C (Paragamian & Wakkinen 2002), but whether and when white sturgeon would spawn in relation to the additional volume of water released from Libby Dam in accordance with the USFWS Recovery Plan had not been evaluated.

The objectives of this study were to assess whether augmented discharge from Libby Dam benefited white sturgeon spawning and to determine how discharge, water temperature and day of the year may interact to trigger white sturgeon spawning. This evaluation could be important in guiding both the timing and water temperature of future discharge augmentation operations at Libby Dam and possibly other dams and systems where white sturgeon populations are in decline (Cochnauer *et al*. 1985; USFWS 1993; UCWSRI (Upper Columbia White Sturgeon Recovery Initiative) 2002).

Study site

The Kootenai River (spelled Kootenay in Canada) is in the upper Columbia River Basin and originates in Kootenay National Park, British Columbia, Canada, flows south into Montana, USA, and Koocanusa Reservoir impounded by Libby Dam at river kilometre (rkm) 352 (Fig. 1). Downstream of Libby Dam, the river then flows northwest into Idaho and then north into Kootenay Lake, British Columbia (rkm 120), before joining the Columbia River at Castlegar, British Columbia. The primary study reach for this investigation was from rkm 228 to 246, the spawning area downstream of Bonners Ferry, Idaho.

Koocanusa Reservoir is the upstream-most water storage impoundment on the Kootenai River; it is isothermic from mid-December to early April and then gradually warms through the spring towards pre-dam normative river temperatures. Atmospheric warming of the discharge enroute to Bonners Ferry is inversely related to discharge during spring. During this investigation, release temperatures during this isothermic period were generally warmer than pre-dam conditions until mid-March and then remained cooler than pre-dam conditions until early May (Partridge 1983).

Methods

Estimated spawning events

Artificial substrate mats (McCabe & Beckman 1990) were used to document white sturgeon spawning from 1994 to 2002 (Paragamian & Wakkinen 2002). Embryonic age in hours of collected white sturgeon eggs was estimated using criteria developed by Beer (1981). White sturgeon spawning dates were estimated using an exponential function with water temperature and embryonic development stage (Wang *et al*. 1985). This method can accurately estimate the age of a white sturgeon egg by ±4 h. The age of white sturgeon eggs was used to estimate the date of spawning events by one or more females. The spawning period for each year was defined by the dates of the first and last spawn events.

Environmental variables

Daily mean river discharge for the spawning season (defined as May 1 to June 30) from 1994 to 2002 was calculated from hourly gauge readings at Leonia, Montana (rkm 270), downstream of Libby Dam (Fig. 1), and daily mean temperature was calculated from hourly temperature measurements at Bonners Ferry, Idaho (rkm 246). Change in discharge during 24 h (1-day Δ discharge) was calculated as the difference in daily means from 1 day to the preceding day. These statistics for the 116 spawning event dates were the basis for spawning event averages for temperature, discharge and 1-day Δ discharge for each of the nine study years.

Thermal conditions in the Kootenai River in Idaho are related to the volume and temperature of water discharged from Libby Dam. In general, lower discharge from the dam allows the river to warm more quickly than higher discharge, and the initial release temperature determines to what extent the river will warm as it discharges downstream, but the interaction of discharge and release temperature had not been quantified. It was important to examine to what extent discharge changes river temperature and the interaction of temperature and discharge on white sturgeon spawning. Linear regression was used to assess whether river temperature was influenced by mean discharge or 1-day Δ discharge for all spawning event dates.

Relationships of environmental variables and spawning

Probability analysis (Zar 1984) was used to determine the probability of spawning from mean daily temperatures and discharges. The probability of spawning (the number of spawning events divided by the number of occurrences of each temperature or discharge increment) was calculated in 0.5 °C increments for mean daily temperature and in 1.0 $m^3 s^{-1}$ increments for mean daily discharge.

Stepwise linear regression was used to assess the relationship of daily mean temperature, discharge and Δ discharge with the dependent variable onset of spawning (Julian day of the first spawn event) for each of the nine study years. In addition to the 1-day Δ discharge, regression analysis also included the 3-day Δ discharge. The 3-day Δ discharges were quantified as the slope of the regression lines for the 3-day time interval preceding the onset of spawning in each year.

Logistic regression analysis was used to determine the best models for predicting spawning from Julian date, mean temperature, mean discharge, 1-day Δ discharge, temperature code (8 °C and above or below 8 °C) and Δ discharge for the 3, 7 and 14 days preceding the spawn. The 7-day and 14-day Δ discharge were quantified as the slope of the regression line for 7-day and 14-day time intervals. The 7-day and 14-day Δ discharge were not included in the linear regression to assess the onset of spawning described above because discharge data were not available in 1 year to estimate these variables. This analysis was based on 100 spawn events; sixteen events were dropped because of incomplete temperature and discharge data for those dates. Single-variable logistic models were used to evaluate each variable in consideration for the full predictive model. Likelihood ratio tests and a $P \leq 0.25$ were used in variable selection (Hosmer & Lemeshow 1989). The full model was evaluated and further reduced based on the Wald statistics for the regression coefficients (Hosmer & Lemeshow 1989). The final model was evaluated using the Wald statistics for the individual coefficients (significance at $P < 0.05$) and the likelihood ratio test of the full model vs the reduced model.

Final model significance (goodness of fit) and predictive indices (λ_p and τ_p and their statistical significance as measured by the binomial d statistic) were calculated according to the methods described by Menard (1995). λ_p is an index similar to Goodman and Kruskal's lambda for evaluating contingency tables (Menard 1995). λ_p (based on the mode of the dependent variable as the predicted value for all cases) is a proportional reduction in error measure like R^2 when it is positive, but when negative indicates a proportional increase in error. It is most useful in evaluating prediction models but does not assume heterogeneity of the sample. λ_p values >0.5 indicate a substantial reduction in the error of predicting outcomes as 1 or 0 through the use of the model. τ_p is most useful in classification models where heterogeneity is assumed and imposes a further constraint that the model should classify as many cases into each category as are actually observed in each category. A value of 1 for τ_p indicates all cases are correctly classified and a negative value indicates the model does worse than expected in predicting the classification of cases (Menard 1995). The classification table (predicted and observed values of the dependent variable for the cases in the analysis) for the model was also examined as an indication of how accurately the model predicted group membership.

Results

White sturgeon spawned each year of the study, and white sturgeon egg samples were collected from 116 spawning events (Table 1). Mean daily discharges for spawning event dates ranged from 250 $m^3 s^{-1}$ in 2001 to 1017 $m^3 s^{-1}$ in 1997 (Table 2). Temperatures during spawning events ranged from 6.6 to 16.9 °C.

Discharge augmentation from Libby Dam for white sturgeon was provided in 6 of the 9 years of study (Table 1). In two of the three non-augmented years (1996 and 2002), water volume exceeded the highest

Table 1. Spawning period and discharge conditions during May and June in the Kootenai River, Idaho, 1994–2002

Year	1994*	1995*	1996	1997*	1998*	1999*	2000*	2001	2002
Spawning period	13 May–10 June	23 May–13 June	6 June–25 June	8 June–21 June	6 May–6 June	30 May–19 June	23 May–21 June	25 May–23 June	31 May–30 June
Peak discharge ($m^3 s^{-1}$), date	582.9 7 June	943.6 17 May	1293.8 2 June	1161.5 6 June	969.0 27 May	1005.4 16 June	884.2 13 June	392.6 14 May	1155.0 30 June
Peak discharge before spawning period ($m^3 s^{-1}$)		6 days	4 days	2 days				11 days	
Discharge at first spawn event ($m^3 s^{-1}$)	308.1	811.4	1021.4	1112.4	421.5	511.9	459.1	383.3	786.3
Peak discharge during spawning period ($m^3 s^{-1}$), date	582.9 7 June	864.4 30 May	1117.9 8 June	1122.9 11 June	969.0 27 May	1005.4 16 June	884.2 13 June	383.3 25 May	1155.0 30 June

*Augmentation year.

Table 2. Discharge conditions for white sturgeon spawning event dates in the Kootenai River downstream of Libby Dam, 1994–2002. Values in parentheses are standard deviations

Year	1994	1995	1996	1997	1998	1999	2000	2001	2002
Mean discharge ($m^3 s^{-1}$), range	427.7(93.3) 285.3–582.9	809.5(33.5) 741.9–864.4	952.3(90.4) 841.1–1117.9	1017.2(162.9) 638.6–1122.9	591.1(172.4) 312.4–969.0	580.3(226.0) 349.8–1005.4	526.1(244.6) 294.6–851.3	250.3(90.8) 163.7–383.3	525.8(174.6) 614.2–1155.0
Mean 24-h discharge change ($m^3 s^{-1}$), range	6.26(28.0) 0.9–75.3	−0.02(19.2) 0.02–39.6	−19.4(48.7) 1.6–161.8	−37.8(65.4) 2.0–162.0	−2.4(94.9) 3.7–292.3	15.96(166.6) 3.1–362.1	−10.9(13.8) 2.0–32.5	−7.9(16.8) 1.8–30.4	1.87(58.0) 12.6–121.9

tier, and the third year (2001) was a drought year with no discharge augmentation possible.

White sturgeon spawning commenced before discharge augmentation began in 4 of 6 years with augmented discharge [1994, 1998 (see Fig. 2 for 1998), 1999 and 2000]; spawning began 2–6 days after the peak augmented discharge in the other 2 years when discharge augmentation occurred (1995 and 1997; Table 1). Spawning began 4–11 days after the primary peak discharge in the two high-water years (1996 and 2002) when no flow augmentation occurred. In the drought year with no augmentation, the onset of spawning occurred 29 days before the peak in discharge.

Linear regression analysis indicated a statistically significant relationship between mean daily river temperature and mean daily discharge and 1-day Δ discharge ($F_{(2,6)} = 20.29$, $P = 0.002$). The high coefficient of determination ($R^2 = 0.87$) indicated that river temperature below Libby Dam was closely associated with discharge and the 1-day Δ discharge from the dam; higher flows provided cooler water.

Probability analysis indicated the highest probability of spawning (0.48) fell within the 9.5–9.9 °C interval. Although spawning occurred at temperatures as low as 6.5 °C, 93% of the spawning events occurred at temperatures > 8 °C.

Probability analysis of river discharge indicated a high likelihood of spawning (100%) at 75 recorded discharges ranging from 164 to 1155 $m^3 s^{-1}$. Sixty percent of the spawning events were recorded when river discharge was 600 $m^3 s^{-1}$ or higher; discharges > 600 $m^3 s^{-1}$ occurred on 45% of the days during the May–June spawning seasons.

Spawning began as early as 6 May (1998) and as late as 8 June (1997) (Table 1). Of the four environmental

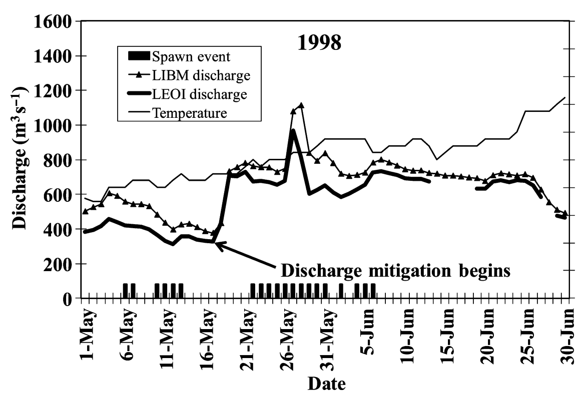

Figure 2. Discharge at Libby Dam (LIBM) and Leonia (LEOI), temperature at Bonners Ferry, and spawning events during May and June 1998 in the Kootenai River at Leonia, rkm 270.

variables considered (mean daily temperature, mean daily discharge, 1-day Δ discharge and 3-day Δ discharge), only mean daily discharge was significantly related to spawning onset (R^2 = 0.60, $F_{1,7}$ = 10.69, P = 0.014). Spawning occurred later in years of greater mean daily discharge.

Mean temperature, mean discharge and 1-day, 3-day, 7-day and 14-day Δ discharge measurements were available for 100 spawning events during the May to June spawning seasons during 1994–2002. Logistic regression indicated a statistically significant relationship between the probability of detecting a spawning event and Julian date, mean daily temperature code, mean 1-day Δ discharge and the 7-day Δ discharge (model χ^2 = 45.34, P < 0.001). The overall proportion of the cases correctly classified by the model was high (77%) due primarily to the large number of correctly predicted no-spawning event cases (347 of 356; Table 3). However, the model reduced the error of prediction (vs the intercept only model using no independent variables) by only 9.45%. The predictive indices were small, suggesting at best a weak, but statistically significant, relationship between the dependent and independent variables (τ_p = 0.34, d = 5.24, P < 0.000) and at worst a model that slightly increased the error of prediction over the intercept only model (λ_p = −0.03, d = 0.34, P = 0.367). Only 6% of the spawning event–occurred cases were correctly predicted. This had little impact on the overall goodness of fit of the model as measured by the model χ^2 because of the large number of correctly predicted cases (347) when spawning did not occur. It did have substantial impact by reducing the indices of predictive efficiency, λ_p and τ_p.

Discussion

Time of spawning of white sturgeon in the Kootenai River varied among years and occurred before discharge augmentation from Libby Dam began in 4 of 6 years with augmented discharge. The spawning response in the other 2 years with augmented discharge was not immediate and occurred 2 and 6 days after discharge augmentation commenced. The only measurable benefit of the discharge augmentation from Libby Dam during this study resulted in maintenance of minimum threshold discharge for spawning white sturgeon. Therefore, onset of spawning of Kootenai River white sturgeon was likely independent of additional discharge provided by augmented discharge from Libby Dam.

Table 3. Final model classification table (percentages in parentheses)

Observed event	Predicted event: No spawn	Spawn	Total
No spawn	347 (97.5)	9 (2.5)	356
Spawn	94 (94)	6 (6)	100
Total	441	15	456

In a previous study, mean daily temperature and river stage were significant predictors of female white sturgeon spawning migration, but temperature was the more significant predictor of the two variables (Paragamian & Kruse 2001). Paragamian and Kruse (2001) found temperatures ranged from 6.6 to 10.7 °C during migration and averaged 8 °C during the spawning migrations of females. Spawning was also found to occur soon after the arrival of females to the spawning reach. Paragamian and Wakkinen (2002) found that after migration to the spawning reach and the onset of spawning, the temporal distribution of the detected spawning events appeared to depend on the relative stability of temperature, which is also related to discharge management from Libby Dam. In this study, a significant relationship was found between discharge from Libby Dam and river water temperature: higher discharges lowered river temperature and white sturgeon tended to spawn later. The years or periods of spawning within a year with the most recorded spawning events (1994–2000) were associated with temperatures (7.5–14 °C) that were stable, increasing or when changes were moderate (decreases of 0.7 °C or less). In the current study, as with the 1994 to 2000 study, the highest probability of spawning (0.48) was for the 9.5–9.9 °C interval, and 93% of spawning events occurred when water temperature was above 8 °C.

White sturgeon spawning occurred at a wide range of discharges in the 1994–2002 study, suggesting that once a temperature threshold of about 8 °C was met, the spawning migration began and spawning was likely to occur. Paragamian and Wakkinen (2002) found a discharge threshold for spawning of about 350–400 $m^3 s^{-1}$. However, the majority of white sturgeon spawning events during this study (60%) occurred at discharges of 600 $m^3 s^{-1}$ or greater even though such discharges occurred only 45% of the time. In the Columbia River below the Waneta Dam, British Columbia, Golder (2005) failed to find any definitive effects of temperature and discharge on white sturgeon spawning. The current study found that mean daily discharge was the only variable significantly related to the onset (first date) of spawning. White sturgeon spawning in the Kootenai River, although statistically related to mean daily temperature and the increasing or decreasing trends in discharge during the previous 7 days, could not be reliably predicted by the combination of variables. The poor predictive performance of the logistic model, in spite of its statistical significance, may have been due in part to sample size and the underlying assumption of 100% detection of spawning and the response variable selected. The model was based on 456 cases, of which only 100 were detected spawning events. This resulted in 3.5 times more instances of non-spawning used in model building which may have skewed the results. The determination of spawning and non-spawning dates for each of the 456 cases was based on the assumption that only those dates when eggs were collected were considered spawn event dates. The possibility exists that some spawning events were missed because of sampling intervals and mat placement for egg collection. Additionally, while back-calculating egg collections to determine spawn dates may provide more concrete evidence of spawning than telemetry data, actual documentation of spawning activity as it occurred would be preferable when trying to relate it to specific environmental variables. Refinements to improve the predictive performance of the model should still make it a useful tool for resource managers. These could include adjustments to account for the skewed ratio of non-spawning to spawning events, methods to determine what portion of eggs and therefore spawn events are missed through mat sampling and consideration of methods to better determine when and where spawning occurs.

Given what has been learned in previous studies about temperature and discharge in the Kootenai River (Paragamian & Wakkinen 2002) and from this investigation, it appears that after temperature and discharge exceed spawning migration and spawning thresholds, minor fluctuations in temperature (<0.7 °C) had little or no impact on white sturgeon spawning. Further, augmented discharges had little benefit to white sturgeon other than maintaining a minimum discharge for white sturgeon spawning. White sturgeon were found to abandon the spawning reach when river discharge fell below 300 m^3 s^{-1} (Paragamian & Kruse 2001).

Evaluation of the selective withdrawal system at Libby Dam indicates that it can be a useful system to improve white sturgeon spawning. This system has been managed to meet downstream temperature targets in the Kootenai River during the reservoir's stratification process in spring. This was accomplished through the operation of bulkheads that control the elevation and temperature of water released from the dam. The thermal conditions in Lake Koocanusa at Libby Dam typically lag behind seasonal weather conditions by a month or more because of the long residence time and thermal inertia of the reservoir. The thermal water conditions at Libby Dam typically reach minimum temperatures during late March or early April characterised by a uniform temperature less than 4 °C (isothermic). The capability to manage release temperatures begins to develop with the onset of thermal stratification during late April and into May. The initial stratification can be weak and often short lived as weather systems disrupt the thermal structure. The strategy to operate the selective withdrawal system to release the warmest water available in the forebay for white sturgeon spawning downstream during the onset of stratification often resulted in abrupt fluctuations in release water temperatures. The findings in this study suggest that more consistent spawning conditions would be achieved by managing dam operations to achieve desirable discharge and temperature conditions that coincided with white sturgeon arrival to the spawning reach. Selective withdrawal temperature operations since these data were collected and analysed have shifted to target the most consistent water temperatures of 8 °C or warmer without abrupt temperature declines during the migration period of spawning females.

Acknowledgments

This work reflects the dedicated efforts of many people involved in white sturgeon sampling projects over the years including Kim Apperson, Pat Marcuson, Pete Rust, Gretchen Kruse, Dorothy Laude, Genny Hoyle and Vint Whitman of the Idaho Department of Fish and Game; Sue Ireland, Jack Siple, Robert Aitken, Ralph Bahe, Chris Lewandowski, Eric Wagner, Dennis David, and Larry Aitken of the Kootenai Tribe of Idaho; and Colin Spence, Don Miller, and Matt Neufeld of the British Columbia Ministry of Environment. Thanks to Dan Schill of the Idaho Department of Fish and Game for editorial review. Special thanks to Greg Hoffman of the US Army Corps of Engineers and Brian Marotz of the Montana, Fish Wildlife and Parks for their helpful comments and patience. Funding was provided by the Bonneville Power Administration.

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