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Spawning Habitat of Kootenai River White Sturgeon, Post-Libby Dam

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Abstract.—The Kootenai River white sturgeon *Acipenser transmontanus* has been isolated from other white sturgeon populations for over 10,000 years, Bonnington Falls in British Columbia, Canada, creating the isolation. Libby Dam, constructed in 1972, modified the flow and temperature regime of the river, which affected spawning and recruitment of white sturgeon. Kootenai River white sturgeon are only known to spawn in a reach near Bonners Ferry, Idaho, 100 km downstream from the dam. In 2 of 8 years of study, only 15 white sturgeon eggs were collected over gravel–cobble substrate. However, in the other 6 years, 1,193 eggs were collected over sand substrate; these areas usually exceeded 5 m in depth, were within the main channel, and had water velocities of 0.2–1.0 m/s and temperatures of 8.5–12°C. In general, these characteristics differed from optimum white sturgeon spawning habitat in the Columbia River, where velocities average 0.8 m/s, water temperatures are 12–17°C, and gravel–cobble substrate is available. Spawning over sand substrate might contradict survival strategies because white sturgeon have an adhesive egg to which sand adheres. Differences in spawning habitat may be an outcome of behavioral divergence or disruption to environmental cues but was probably caused by preferred habitat no longer being available. Recovery of Kootenai River white sturgeon will depend primarily on continuation of mitigated flows for spawning migrations, suitable spawning habitat, and ultimately survival of eggs and larvae. It is unknown at this time whether recent spawning alone will lead to sufficient recruitment to help recovery of the population, but if it does not recruit substantial year-classes, we believe consideration must be given to measures that would provide coarser spawning substrates and warmer water temperatures.

Sturgeon (Acipenseridae) populations are threatened worldwide by habitat loss and overexploitation (Birstein 1993). Habitat loss is often due to hydroelectric and flood control dams that have affected sturgeon spawning migration, nursery habitat, and recruitment (Alekperov 1969; Khoroshko 1972; Votinov and Kas'yanov 1978; Parsley 1991; Parsley and Beckman 1994; Auer 1996; Nilo et al. 1997). The importance of spawning habitat to the persistence of sturgeon populations has been well established (O'Herron et al., no date; Heidt and Gilbert 1978; Buckley and Kynard 1981, 1982; Parsley et al. 1993; McCabe and Tracy 1994; Gard 1996; Krykhtin and Svirskii 1997; Williot et al. 1997; Zhuang et al. 1997). The white sturgeon *Acipenser transmontanus* is the only sturgeon endemic to Idaho and is found in the Snake, Clearwater, Salmon, and Kootenai rivers (Simpson and Wallace 1982). Habitat changes due to hydroelectric and flood control dams have also affected sturgeon populations in Idaho by limiting spawning habitat and recruitment (Cochnauer et al. 1985; Paragamian et al. 1996; Lepla and Chandler 1997).

The Kootenai River white sturgeon is a genetically distinct stock (Setter and Brannon 1990), isolated from other white sturgeon populations by the Bonnington Falls in British Columbia, Canada, for about 10,000 years (Northcoat 1973). A companion study (Paragamian and Kruse, this issue) also determined this sturgeon has unique behavioral characteristics; it is active at 6°C, several degrees cooler than the activity threshold for Columbia and Snake river white sturgeon. The Kootenai River white sturgeon also has a unique spawning pattern of a "short two step migration" (Bemis and Kynard 1997), migrating from the lower river and Kootenay Lake, British Columbia, during autumn to staging reaches and then migrating in spring to the spawning reach near Bonners Ferry, Idaho (Figure 1).

The Kootenai River had a history of flooding, and in 1966 the U.S. Army Corps of Engineers (USACE) began construction of Libby Dam near Jennings, Montana, for flood control and hydropower (Figure 1). The dam was completed in 1972, and the reservoir behind the dam (Lake Koocanusa) was filled in 1973. Soon after that, the white sturgeon population became recruitment limited,

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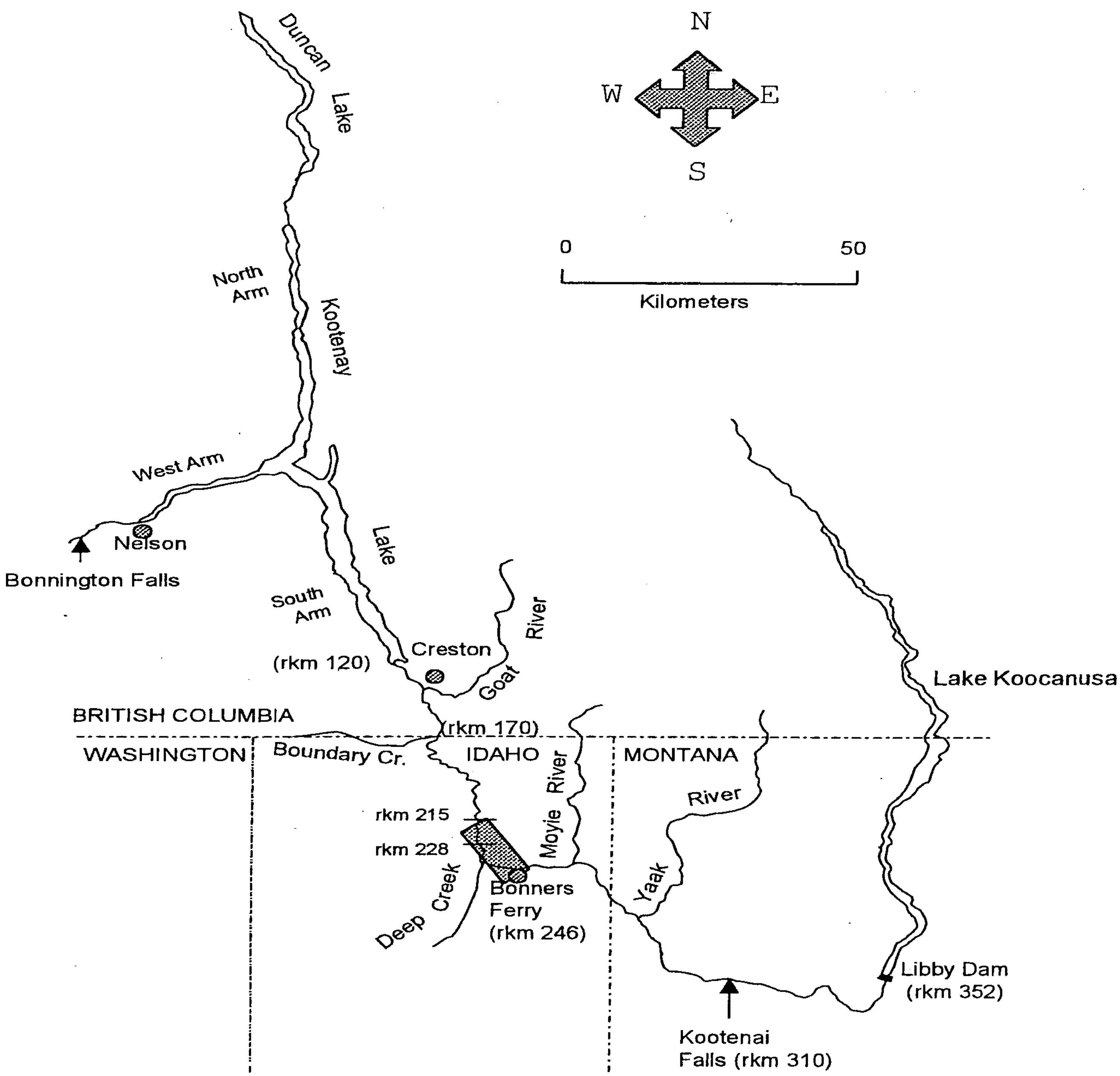

FIGURE 1.—Geographic reference points related to our spawning habitat study of Kootenai River white sturgeon. The river distances (in river kilometers, rkm) indicated are from the northernmost reach of Kootenay Lake.

and juvenile sturgeon became scarce (Partridge 1983; Apperson 1990). The physical and chemical attributes of the river after construction of Libby Dam changed from the historical conditions. Historically, flows during the sturgeon spawning period were 1,416–2,832 m^3/s, but after Libby Dam began to operate, peak flows were generally 250–450 m^3/s. In addition, the river temperature regime was about 1°C cooler in the summer and 4°C warmer in winter (Partridge 1983), and the river was less productive (Woods 1982; Snyder and Minshall 1995).

To prevent further decline and aid in the recovery of Kootenai River white sturgeon, it became critical for managers to initiate measures to restore migration, spawning, and rearing habitat; however, the particular spawning-related inadequacies of habitat were unknown. From 1991 through 1993 the USACE provided some augmented flow during spring, but in general it was insufficient to restore the natural flow regime during the spawning season. Because of its unique genetic status and imperiled population status, on September 6, 1994, the Kootenai River white sturgeon population was added to the Federal Registry, under the Endangered Species Act (ESA), as an endangered species. After that (1995–present), flow augmentation for sturgeon spawning was greater in volume and usually more timely.

Recovery efforts for Kootenai River white sturgeon are focused on providing higher flows during the spring spawning period, establishing the timing and location of spawning, and documenting wild juvenile abundance. The objective of our investigation was to identify the actual and potential spawning habitats of Kootenai River white sturgeon. Initially, preferred white sturgeon spawning habitat in the Kootenai River was assumed to be similar to that of Columbia River white sturgeon. Instream flow (incremental methods) and substrate analysis (Apperson 1990) indicated the reach of river with gravel–cobble substrate above Bonners Ferry (rkm 245) provided spawning habitat similar to that used by white sturgeon in the Columbia River (Parsley and Beckman 1994). Access to and use of this habitat would thus indicate effective mitigation.

Study Site

The Kootenai River is in the upper Columbia River basin. The river originates in Kootenay National Park, British Columbia, flows south into Montana and turns northwest at river kilometer (rkm) 352.4 (Figure 1). At Libby Dam the river traverses west over Kootenai Falls and into Idaho. Kootenai Falls, 40 km below Libby Dam, is thought to be an impassable barrier to white sturgeon. As the river flows through the northeast corner of the Idaho panhandle, there is a gradient transition at Bonners Ferry. Upriver from Bonners Ferry the channel has an average gradient of 0.6 m/km, and the velocities are often higher than 0.8 m/s. There is a braided transition reach from the Moyie River to Bonners Ferry. Downriver from Bonners Ferry (rkm 244.5) velocities slow to usually less than 0.4 m/s, average gradient is 0.02 m/km, the channel deepens, and the river meanders through the Kootenai Valley.

From 1991 through 1998 we sampled the river from rkm 215 to 258.5. We divided this reach into 12 sections. After 1996 we restricted sampling to rkm 228–247.7 because a companion telemetry study (Paragamian and Kruse, this issue) indicated that white sturgeon adults during the spawning season were located within rkm 228–240 and rarely rkm 245–246. One of the 12 sections was above rkm 247.7 and another was below rkm 228.0, leaving 10 sections within rkm 228–246. The two sections from rkm 244.7 to 247.7 had a gravel–cobble substrate; the two reaches from rkm 240.6 to 244.6 were composed of a shallow (Paragamian et al. 1997) depositional area with one deep pool. The remaining four sections (rkm 228–240.5) were composed of sand substrate and numerous deep pools (Paragamian et al. 1997).

Methods

White sturgeon egg collections and effort.—We used artificial substrate mats (McCabe and Beckman 1990) to examine white sturgeon spawning from 1991 to 1998, based on the premise that our egg sampling method would accurately document the location of spawning and enable spawning habitat to be measured. This premise seemed reasonable because white sturgeon are broadcast spawners and their eggs sink immediately and are adhesive for a short time after spawning (Stockley 1981; Brannon 1984; Cherr and Clark 1985; Wang et al. 1985). Previous studies of sturgeon spawning habitat also depended on these biological characteristics, and some used similar sampling methods (Kohlhorst 1976; Buckley and Kynard 1981, 1982; McCabe and Beckman 1990; McCabe and Tracy 1994; Parsley and Beckman 1994; McKenzie and Hildebrand 1996; Marchant and Shutters 1996; Lepla and Chandler 1997).

Sampling mat placement, including deployment within staging reaches, was done in a variety of configurations to help identify white sturgeon spawning locations. In 1991, groups of three mats were randomly placed in gravel–cobble substrates within rkm 244.7–255. Using the size criteria of Parsley and Beckman (1994), substrate was verified, by visual inspection from boat and scuba diving transects, to be gravel–cobble above rkm 244.7 and predominantly sand below (Apperson 1990). These observations were supported by acoustic sub-bottom profiles of the Kootenai River within rkm 227–246 (Morlick 1996; Paragamian et al. 1998). In 1992 and 1993, sampling mats were used within rkm 226–259, in randomly distributed groups of three to five. In 1994 mats were set every

TABLE 1.—Mat sampling effort (in mat days) in up to 12 study sections (in river kilometers, rkm) 1991 through 1998.

Study section (rkm)	Mat days by year							
	1991	1992[a]	1993	1994	1995	1996	1997	1998
<228.0	0.0	134.3	0.0	0.0	301.0	0.0	0.0	0.0
228.0–229.5	0.0	0.0	0.0	422.2	574.1	236.9	406.5	590.8
229.6–231.5	0.0	106.8	188.9	490.4	627.1	37.9	391.9	482.8
231.6–233.4	0.0	0.0	0.0	3.0	124.0	419.1	388.0	410.9
233.5–234.7	0.0	0.0	0.0	8.9	115.0	233.5	545.1	458.6
234.8–237.5	0.0	0.0	130.8	356.9	600.1	756.9	666.3	697.0
237.6–240.5	0.0	0.0	58.7	367.7	151.0	144.0	513.8	401.1
240.6–243.9	0.0	0.0	0.0	329.3	124.1	194.7	358.1	255.5
244.0–244.6	0.0	41.8	0.0	163.2	177.0	340.5	0.0	0.0
244.7–246.6	124.2	264.5	650.8	259.6	484.0	1,840.5	804.7	304.8
246.7–247.7	119.4	33.8	158.8	0.0	0.0	244.4	181.1	157.4
>247.7	82.0	243.7	545.2	0.0	0.0	0.0	0.0	0.0
Total	325.6	824.9	1,733.2	2,401.3	3,277.6	4,448.3	4,255.6	3,758.8

[a] An additional 50.3 mat days of effort occurred, but the locations were not documented.

0.5 km within rkm 228–245.6. In 1995, mats were distributed within rkm 215–246 to sample a variety of habitats, including three staging areas. In 1996, mats were distributed primarily in the thalweg (rkm 228–247.7) because in 5 years of sampling, no eggs were ever collected near the river margins. In 1997 and 1998 a standardized sampling regime was followed such that mats were placed (rkm 227 through 247) based on the location and density (high, medium, and low) of adult fish (Paragamian et al. 1997). Mats were usually set from mid-May through mid-July. We deployed 70–100 mats each season; mats were pulled and examined for the presence of eggs weekly in 1991, every 2–13 d in 1992 and 1993, and daily from 1994 to 1998. Eggs were removed from mats and stored in labeled vials containing formalin or alcohol solution.

Catch per unit of effort (CPUE; eggs·mat^{-1}·h^{-1}) was used to determine differences in catch between sections. We used two-way analysis of variance (ANOVA) and analysis of residuals to determine if the data were normally distributed. Then we used Friedman's nonparametric two-way ANOVA to determine if there were differences in CPUE between the 12 sections. Hours of effort per egg caught (HEPE) was also calculated as an alternative measure of egg catch success.

Age of eggs.—Embryonic ages (stage) of white sturgeon eggs were distinguished visually with a dissecting microscope at 120× power and aged by using embryonic criteria developed by Beer (1981). White sturgeon spawning dates (±4 h) were back-calculated from all viable eggs by using an exponential function involving water temperature and embryonic development, as described by Beer (1981) and Wang et al. (1985). After 1994, when egg mats were checked daily, we used the age of white sturgeon eggs as a general index to determine how long they were available for capture.

Habitat at egg collection locations.—Time, depth, substrate, water temperature, and location (to 0.1 km) were recorded at deployment and retrieval for each mat. Velocities were measured with a Marsh McBirney model 2000 or model 201, and mean water column velocities were calculated at most egg collection sites. Environmental data were compiled; we compared spawning temperatures, egg collection depths, and mean column velocities at egg collection locations to habitat suitability curves developed by Parsley and Beckman (1994).

Results

White Sturgeon Egg Collections and Effort

We expended a total of 21,025 mat days (one 24-h set for one mat) or 504,607 h of mat sampling effort between 1991 and 1998 to verify natural spawning of white sturgeon in the 12 study sections of the Kootenai River (Tables 1, 2). The greatest amount of effort was in 1996, when over 4,448 mat days (106,759 h) of effort were logged. The amount of effort above rkm 244.7, where we expected white sturgeon to spawn, varied each year, but 2,085 mat days (50,040 h) of effort were logged in 1996 and 986 mat days in 1997 (23,659 h) (Table 1).

Few eggs were collected between 1991 and 1993, when the only mitigative flows provided for white sturgeon spawning were minimal and sampling effort was less than in the following years of the study. Thirteen eggs were collected on July

TABLE 2.—Sample dates, total effort, number of eggs collected, catch per unit of effort (CPUE; eggs·mat^{-1}·h^{-1}) and hours of effort per egg caught (HEPE) for all artificial substrate mat sampling sites in the Kootenai River, Idaho, 1991–1998; mean, standard deviation, and minimum (min) and maximum (max) values (NA = not available) for depth, midcolumn velocity, and temperature at all sites and egg collection sites on estimated spawning dates are also listed.

Year	Number of mats: Set	Number of mats: With eggs	Number of eggs	Site	Velocity (m/s): Mean	Velocity (m/s): SD	Depth (m): Mean	Depth (m): SD	Temperature (°C): Mean	Temperature (°C): Min	Temperature (°C): Max	Total hours sampled	CPUE (HEPE)
1991	62	1	13	Egg sites	NA		NA		13.0	13.0	13.0	7,813.5[a]	0.0017
				All sites			NA		11.2	9.0	14.0		(601)
1992	121	0	0	Egg sites								19,797.6	0
				All sites			5.3	2.4	14.1	12.0	18.5		
1993	354	2	2	Egg sites	NA		3.0[b]		NA	NA	NA	41,596.5	0.0001
				All sites	0.83[c]	0.32	4.1	3.2	14.8[d]	12.0	18.3		(20,799)
1994	1,940	37	213	Egg sites	0.25	0.17	8.5	1.5	NA	NA	NA	57,630.2	0.0037
				All sites			7.7	2.4	11.9[e]	8.6	16.2		(271)
1995	2,111	37	162	Egg sites	0.19	0.13	11.0	1.9	11.3	8.5	14.0	78,662.9	0.0021
				All sites			9.9	3.0	9.7	7.0	14.0		(486)
1996	4,242	44	349	Egg sites	0.22	0.08	11.6	3.1	11.5	9.5	13.5	106,758.5	0.0033
				All sites			8.4	4.2	11.3	6.0	18.0		(306)
1997	3,832	14	75	Egg sites	0.67	0.15	13.3	2.9	11.8	10.0	13.0	102,133.4	0.0001
				All sites			9.1	3.4	11.8	9.0	16.0		(1,361)
1998	2,212	60	393[f]	Egg sites	0.61	0.17	11.4	2.8	9.9	9.0	12.5	90,211.6	0.0044
				All sites			9.8	3.3	10.6	8.0	14.0		(230)

[a] Total hours include estimated times (based on surrounding mats) for those with unknown set and pull times.
[b] Depth recorded for only one mat.
[c] Velocity sampled at representative sites from river kilometer 229.9–257.6 from May 20–June 28 by Idaho Department of Fish and Game.
[d] Temperatures not recorded; maximum daily from U.S. Army Corps of Engineers gauge at Porthill, Idaho (May 18–July 12).
[e] Temperatures not recorded; maximum daily from U.S. Army Corps of Engineers gauge at Porthill, Idaho (May 10–July 8).
[f] An additional 90 eggs were caught in the six experimental egg mats and not included in this table.

3, 1991, at about rkm 245.5, no eggs were collected in 1992, and two eggs on both June 7 and 15, 1993, were collected (rkm 244.9 and 246; Table 2; Figure 2). Flow at Bonners Ferry for 1991 on the single spawning date was 374 m^3/s, whereas flows on the two 1993 spawning dates were about 545 and 547 m^3/s.

We collected many more eggs from 1994 through 1998 when mitigative flows were higher and our effort was greater (Table 2; Figure 2). All eggs were collected between rkm 228 and 240.5. In 1994, we collected 213 eggs from May 15 to June 20; in 1995, 162 eggs from May 22 to June 17; and in 1996, 349 eggs from June 8 to June 30. The highest total catch of eggs (262) at any of the study sections from 1991 to 1998 occurred in 1996 at the section from rkm 237.6 to 240.5. High flows in 1997 compromised sampling because debris was transported into float lines and mats were buried by shifting sand. As a result, the lowest number of eggs collected after ESA listing of white sturgeon occurred in 1997, namely, 75 eggs collected from June 5 to June 24. A total of 393 eggs were collected in 1998 from May 6 through June 6. No eggs were ever collected in the transition reach (rkm 240.6–244.6). Ranges in average daily flow at Bonners Ferry during the spawning seasons were 428–582, 754–891, 891–1,260, 742–1,266, and 400–1,175 m^3/s for 1994 through 1998, respectively.

We examined the 1991–1998 data, excluding 1992, and plotted CPUE (Figure 2), as well as a plot of the residuals from the two-way ANOVA, using study section and year. This indicated the data were not distributed normally, which made the results of the ANOVA suspect. We then used Friedman's nonparametric two-way ANOVA. The results of this test indicated that CPUE between study sections was statistically different for all years combined ($P = 0.005$). The highest CPUE (about 0.0255 eggs/h) occurred in 1995 at the section from rkm 234.8 to 237.5 (Figure 3). The CPUE between years for all sections combined was not statistically significant ($P = 0.258$).

Age of Eggs

Viability of the white sturgeon eggs collected was 63% in 1994 ($N = 135$), 78% in 1995 ($N = 127$), 74% in 1996 ($N = 256$), 77% in 1997 ($N = 57$), and 87% ($N = 420$) in 1998; the unweighted average was 76%. Many of the eggs we examined during the study were coated with sand, but that

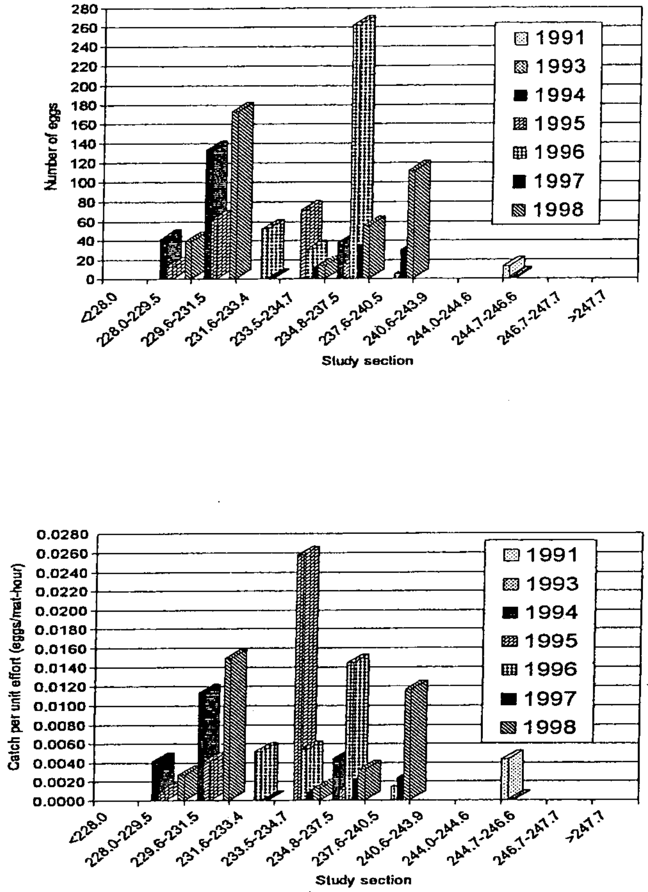

FIGURE 2.—Number of white sturgeon eggs caught each year (1991–1998) within the study sections sampled in the Kootenai River, Idaho (upper panel) and attendant catch per unit effort (eggs/mat-hour; lower panel).

did not appear to affect their viability. Age of eggs provided an index to the approximate length of time they were at large in the river. Aging of eggs indicated that most were recently spawned; i.e., about 96, 80, 62, 76, and 82% (1994 to 1998, respectively) were 2 d old or younger. Many of the eggs were only a few hours old when collected; 9–30% of the eggs each year were less than 5 h old and 25–69% were less than 15 h old (Figure 3).

Habitat at Egg Collection Locations

Our results indicated most spawning took place within rkm 227–240 (Figure 2). Although sampling mat effort for most years was distributed from rkm 227 to 247, no eggs were ever collected in the shallower and lower velocity reach of river from rkm 240 to 244.5.

Spawning substrate at egg collection sites in 1991 and 1993 were gravel–cobble (rkm 245.5). However, substrate at egg collection sites from 1994 through 1998 consisted of sand and pockets of fine gravel (rkm 227–240; Parsley and Beckman 1994), as substantiated by periodic scuba diving during and after the spawning season.

Average 1991 and 1993 temperatures during the only documented times of white sturgeon spawning were 13°C and about 14.8°C, respectively. Temperatures during spawning in 1994 are thought to have been about 8.6–16.2°C; no data were available at specific egg collection sites for that year, but daily temperatures were available from a USACE gauge near Bonners Ferry. In 1995 temperatures were 8.5–14.0°C; in 1996, 9.5–13.5°C; in 1997, 10.0–13.0°C; and in 1998 about 9–12.5°C (Table 2). Temperatures during spawning of Kootenai River white sturgeon (8.5–12°C) were cooler than the optimum (14–15°C) recorded by Parsley and Beckman (1994; Figure 4).

Depth at the only known spawning location in 1991 was thought to be about 2 m and about 3 m in 1993 (Table 2). All eggs collected from 1994 to 1998 were collected in the vicinity of the thalweg. Water depths at egg collection sites were 4.9–10.7 m in 1994, 7.6–15.5 m in 1995, 6.4–17.4 m in 1997, and 6.7–18.0 m in 1998 and 1999. These spawning depths were similar to those of white sturgeon in the Columbia River (Figure 4).

Mean water column velocities at egg collection sites were 0.9 m/s in 1991 and 0.83 m/s in 1993; means were 0.03–0.53 m/s in 1994, 0.12–0.90 m/s in 1995, 0.08–0.46 m/s in 1996, 0.46–0.94 m/s in 1997, and 0.21–0.94 m/s in 1998 (Table 2). Mean water column velocities and standard deviations for the egg collection sites are presented in Table 2. These velocities were slower than the optimum found for white sturgeon in the Columbia River (Parsley and Beckman 1994; Figure 4).

Discussion

Evaluation of Kootenai River white sturgeon spawning locations and habitat is based on the assumption that eggs were collected within the vicinity of the spawning site. Several measures of white sturgeon behavior, spawning location, age of eggs, and companion studies support this assumption. As previously mentioned, white sturgeon eggs are adhesive initially and demersal (Stockley 1981; Brannon 1984; Cherr and Clark 1985; Wang et al. 1985). Spawning above rkm 247

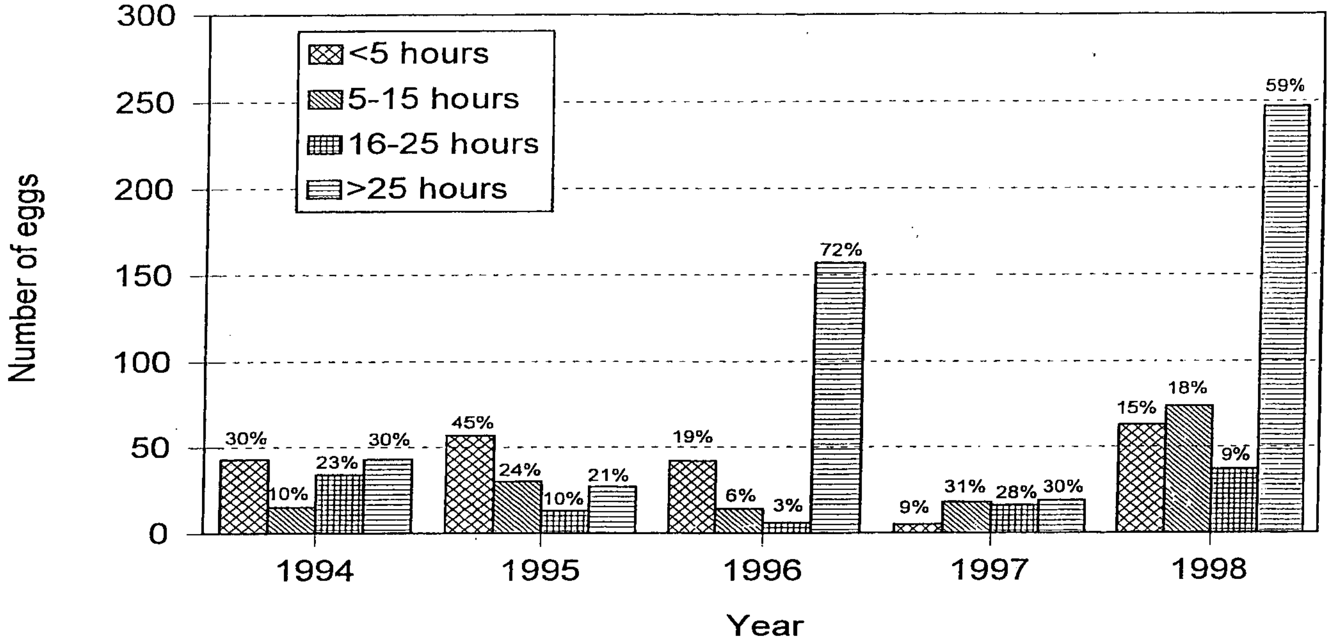

FIGURE 3.—Yearly (1994–1998) numbers of white sturgeon eggs collected in the Kootenai River and their distribution among four egg age categories (<5, 5–15, 16–25, and >25 h).

is probably very unlikely. Sampling by the Kootenai Tribe of Idaho (1993–1995) with D-rings and egg sampling mats upstream of our study sections composed of gravel–cobble (rkm 246–267) did not produce any white sturgeon eggs (Anders 1993, 1994, 1995).

Downstream drift of eggs from the downstream-most gravel–cobble section within our sampling area (rkm 244.5–247) to the sand section furthest upstream (rkm 240) is also unlikely because no eggs were ever captured in the intermediate shallower reach (rkm 240.6–244.6), nor were any eggs ever found downstream of rkm 228 during 1992 and 1995. Furthermore, telemetry of adult white sturgeon in companion studies by boat, fixed-wing aircraft, and two fixed locations with 24-h surveillance receivers indicated few adult sturgeon were ever recorded above rkm 240, and none were ever located above rkm 245.6 (Marcuson et al. 1993, 1994; Paragamian et al. 1995, 1996, 1997, 1998, 1999). White sturgeon eggs in the Kootenai River move with the bottom sediment, but we do not believe the rate of movement affected our measurements of actual spawning habitat (Paragamian et al. 1998). The majority of eggs collected in our study were 2 d or less old. Based on spawning episodes and progressive capture dates, the senior author estimated that white sturgeon eggs in the Kootenai River drift at a rate of about 0.5–1.0 km/d.

Kootenai River white sturgeon eggs were typically collected within the main channel, where water depths usually exceeded 5 m, velocities were 0.5–1.0 m/s, the substrate was sand, and temperatures were usually 8.5–12°C. Most of these characteristics differed from typical white sturgeon spawning habitat in the Columbia River (Parsley et al. 1993; McCabe and Tracy 1994). Parsley and Beckman (1994) developed white sturgeon spawning microhabitat criteria curves (habitat suitability index, HSI) depicting the suitability of temperature, water depth, mean column velocity, and substrate. In the Columbia River the most suitable midwater column velocities for white sturgeon spawning are 1.5–2.3 m/s with temperatures of 12–17°C, although some spawning occurs at cooler temperatures below Bonneville Dam (Parsley et al. 1993) over substrates of clean cobble–gravel. Only depth of spawning by Kootenai River white sturgeon greater than 4 m conformed to the HSI for white sturgeon in the Columbia River. Sturgeon also spawned in a reach with a sand substrate, rated as suboptimal by Columbia River criteria and by life history requirements described by Brannon (1984). Even in the year (1997) of the highest flow

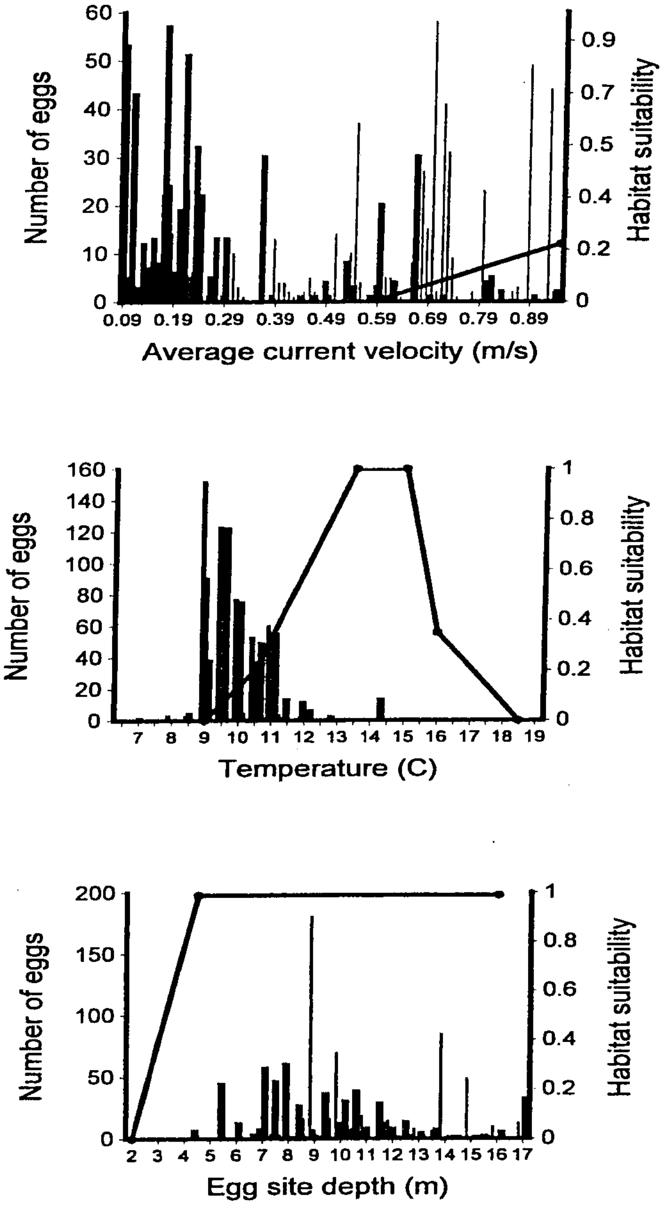

FIGURE 4.—Spawning habitat suitability curves (based on Parsley and Beckman 1994) for white sturgeon in the Kootenai River, Idaho, derived from egg numbers (1991–1998) and the following measured attributes of spawning habitat: mid-column current velocity (top panel), temperature (middle panel), and depth (bottom panel).

since Libby Dam has been in operation (Paragamian et al. 1997), white sturgeon eggs were still found only in the sand reach. Given these differences in white sturgeon spawning habitat, HSI spawning criteria for Columbia River white sturgeon (Parsley and Beckman 1994) are not applicable for post–Libby Dam white sturgeon in the Kootenai River.

White sturgeon spawning over sand substrate appears to be a contradiction to a proposed survival strategy. White sturgeon have adhesive eggs that adhere to coarse substrates. Many of the eggs that we collected were coated in sand, but this did not appear to affect development (Paragamian et al. 1996, 1997). Brannon (1984) believed the adhesion of eggs to cobble and gravel benefit survival of white sturgeon larvae by placing them in proximity to cover after hatching and prevented suffocation by fine sediments. In the Kootenai River, however, eggs and larvae may become buried within large mobile sand dunes (Paragamian et al. 1998). Spawning location of Kootenai River white sturgeon in a reach of river composed of sand was an unexpected result, despite post–Libby Dam flow mitigation, and is a major concern related to survival of eggs and larvae (Paragamian et al. 1996, 1997, 1998). To date only one larval white sturgeon has been captured, and after 5 years of flow mitigation the number of juvenile recruits captured is much lower than anticipated (Paragamian et al. 1996, 1997, 1998).

Other researchers have documented white sturgeon eggs and possible spawning over sand substrate, but in general it is not common. Kohlhorst (1976) found white sturgeon eggs and larvae over sand substrate in the Sacramento River, and some white sturgeon in the Fraser River may also spawn over sand (M. Rosenau, British Columbia Ministry of Environment Lands and Parks, personal communication). Parsley et al. (1993) and McCabe and Tracy (1994) also took a small proportion of their samples of white sturgeon eggs from sand substrate from the Columbia River, but it was not known if these eggs were spawned there or drifted in from the cobble substrates above. As discussed above, we do not believe white sturgeon eggs in the Kootenai River drifted downstream from the gravel–cobble section. Shortnose sturgeon *A. brevirostrum* and Atlantic sturgeon *A. oxyrinchus desoti* are also known to occasionally spawn over sand substrate (Marchant and Shutters 1996; Washburn and Gillis Associates, no date), but survival of these eggs was unknown. However, we do not believe there is a survival benefit to those white sturgeon eggs that are spawned over or drift onto sand substrate because of the low number of recruits we have collected in juvenile sampling (Paragamian et al. 1996, 1997, 1998).

The present spawning location of Kootenai River white sturgeon may be a consequence of post-Libby Dam habitat changes. Preliminary results of a companion study (Paragamian and Kruse, this issue) suggested that location of white sturgeon spawning in the Kootenai River might be caused by a change from the natural spring elevations of Kootenay Lake, British Columbia. In the Kootenai River, white sturgeon form three to four nondiscrete groups of adult spawners during the spawning season. Spawning usually occurred first in the lower portion of the spawning reach (rkm 228–231.5), but as the season progressed, spawning occurred further upstream (rkm 231.6–240.5). However, spawning seldom occurred over the gravel–cobble substrate further upstream near Bonners Ferry (rkm 245+). One possible reason for the spawning location quandary may be the lowering of Kootenay Lake elevation each spring, which began with the completion of Libby Dam (Duke et al. 1999). The Kootenai River has a low gradient, and Kootenay Lake has a backwater affect on the river up to Bonners Ferry. Lowering of Kootenay Lake was a unilateral decision by a Canadian utility company and did not violate any International Joint Commission rulings (Duke et al. 1999). However, the historical elevation of Kootenay Lake before the Libby Dam averaged 534.87 m, whereas after 1972 it has averaged 532.68 m. We examined the movement and spawning location of Kootenai River white sturgeon from 1994 through 1998 and hypothesized sturgeon were spawning in the location of suitable current velocities. However, as the lake elevation rose (to store spring runoff), sturgeon moved further upstream to relocate within the preferred velocities. Where in the water column white sturgeon spawn is not known, but they are thought to be broadcast spawners (Parsley et al. 1993). Spawning activity was thought to have been observed during the 2000 season when a group of six or seven adult white sturgeon was seen rolling and breaching at the surface at about rkm 229 (Jack Siple, Kootenai Tribe of Idaho, personal communication). Within 2 h our crew retrieved an artificial substrate mat located immediately downstream of the activity and removed several recently spawned white sturgeon eggs. Similar observations were reported for white sturgeon on the Columbia River (Parsley et al. 1993). Some researchers believe white sturgeon key on high current velocities for spawning and coarse substrates are the result of the sorting of particles by higher velocities (Parsley et al. 1993). Buckley and Kynard (1981) indicated water velocity and depth might be more important to spawning shortnose sturgeon than depth alone in determining their specific spawning location and substrate. In our study, white sturgeon eggs were found only within the main channel, the streamline of the river, determined by acoustic Doppler current profiles (ADCP) to have the swifter currents (Paragamian et al. 1997; Lipscomb et al. 1998). The ADCP (Lipscomb et al. 1998) also indicated the current velocities in the spawning reach over sand were actually faster than velocities in the location with gravel–cobble substrate (rkm 245.5). Paragamian et al. 1997 also found a significant difference in the distribution of white sturgeon indicating a preference for deeper water. This evidence suggests white sturgeon in the Kootenai River have a preference for the higher velocity water, even though it was associated with sand substrate. We believe some sturgeon may still spawn each year in the gravel–cobble reach, as evidenced by sonic and radio telemetry (Paragamian et al. 1995, 1996, 1997, 1998). However, their numbers were too few for us to detect eggs (e.g., 1991 and 1993, when 13 and 2 eggs were collected, respectively).

Spawning temperature is an additional characteristic that contributes to the unique status of Kootenai River white sturgeon spawning. Kootenai River white sturgeon spawned at temperatures between 8.5°C and 12°C, although Wang et al. (1985) believed the optimum spawning temperature for white sturgeon was 14°C. Because Kootenai River white sturgeon activity occurs at a lower temperature, it is not surprising that their spawning also takes place at lower temperatures (as previously mentioned). This distinguishing behavioral trait and the genetic differences (Setter and Brannon 1990) may be the result of their 10,000 years of isolation from other white sturgeon populations (Northcote 1973) and the shorter growing season in the Kootenai River. While winter temperatures have been substantially different since operation of the Libby Dam, the change in spring temperatures is more subtle (Partridge 1983). An evolving population probably could make adaptive adjustments, through natural selection, enabling it to spawn earlier and thereby make better use of thermal units for growth of age-0 fish. Larger age-0 individuals of some fish species have better overwinter survival than smaller ones because of greater stored energy reserves (Oliver et al. 1979; Shuter et al. 1980; Miranda and Muncy 1987).

Recovery of Kootenai River white sturgeon will depend primarily on the continuation of mitigated flows for spawning migrations and suitable spawning habitat, and ultimately on the survival of eggs and larvae. In recent studies, Kootenai River white sturgeon adults responded to higher mitigated spring flows by migrating to a spawning reach (Paragamian et al. 1995, 1996, 1997, 1998, 1999) and spawning, but they spawned in habitat thought to be unusual for white sturgeon. It is unknown at this time whether these spawning events alone will lead to recruitment sufficient for population recovery. Few wild white sturgeon from flow-test years have been captured (Paragamian et al. 1996, 1997, 1998). Although sturgeon populations with a "short two step migration" often rear in a nursery lake, these recruits could potentially be rearing in Kootenay Lake without our knowledge. However, if they do not recruit substantial year-classes, we believe further analysis of measures to provide better spawning substrates, and perhaps warmer temperatures, may be necessary.

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