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Spawning locations and movement of Kootenai River white sturgeon

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Summary

The Kootenai River white sturgeon *Acipenser transmontanus*, an endangered species, spawns within an 18-km reach in the Kootenai River, Idaho, river kilometer (rkm) 228.0-246.0. Preliminary observations of adult white sturgeon have shown what appeared to be a progressive upstream movement during the spawning season, spawning over sand substrate seldom reaching the typical sturgeon spawning habitat of gravel and cobble located upstream of rkm 244.6. This behavior may be unusual for a white sturgeon population. The primary objective of this paper is to compare, within each spawning season and between seasons, the spatial and temporal pattern of egg collections (as an indicator of spawning location) and the spatial and temporal pattern of suspected spawners, as determined by their movement from 1994 to 1999. Adult white sturgeon were tagged with sonic and radio transmitters. Artificial substrate mats were deployed within three sampling reaches to determine approximate spawning locations and timing in reference to locations of spawners. Eggs were collected 207 different times from 1994 to 1999, including 123 times in the lower reach and 84 times in the middle reach. White sturgeon demonstrated a consistent temporal pattern of shifting spawning location as the season progressed, first spawning in the lower reach and then moving upstream to the middle reach. A total of 1234 contacts of potential spawners were made during May and June for the years 1994-1999. Some spawners were located in as many as four different locations from which eggs were collected within a season. There appeared to be at least five primary spawning locations, most in the vicinity of outside bends. This movement and temporal spawning pattern appears to be unique when compared with published studies on other sturgeon populations. Companion studies indicate that the species is not recruiting despite mitigative measures, and white sturgeon are thought to be spawning in unsuitable habitat. The combination of movement by white sturgeon within this sandy reach during the spawning season and spawning in unsuitable habitat may be contributing to the failure of recruitment. Present measures to recover the population may be inadequate. Further study is needed to determine if this movement pattern is caused by changing water velocities. Also, if historic spawning locations cannot be identified and rehabilitated, then we suggest consideration be given to habitat enhancement measures at the present spawning locations.

Introduction

The Kootenai River white sturgeon, *Acipenser transmontanus*, was given endangered species status in Idaho and Montana, USA, on September 6, 1994. This population of white sturgeon received special status because it became recruitment limited, most notably after completion of the Libby Dam by the US Army Corps of Engineers (USACE) in 1972 (Partridge, 1983; Apperson and Wakkinen, 1992) (Fig. 1), and because the population is genetically distinct from other white sturgeon in the Columbia Basin (Setter and Brannon, 1990). Operation of the Libby Dam modified the Kootenai River flow pattern by lowering flows during spring when white sturgeon spawn (Duke et al., 1999). Under provisions of the Endangered Species Act, an international multi-agency Kootenai River White Sturgeon Recovery Team (KRWSRT) was formed to develop and implement a recovery plan (Duke et al., 1999). Two of the main recovery measures are to (1) augment spring flows for spawning and early life stage rearing and (2) implement a conservation aquaculture (Ireland et al., 2002) and breeding plan (Kincaid, 1993) to prevent extinction (Duke et al., 1999). Our main task was to evaluate augmented flows and assess affects on white sturgeon movement, spawning, and recruitment.

Each autumn and spring, Kootenai River white sturgeon follow a ‘short two-step’ migration pattern (Bemis and Kynard, 1997) from the lower river and Kootenay Lake, British Columbia (BC), to staging reaches downstream of Bonners Ferry, Idaho (Fig. 1). As river stage rises and temperature increases, adult sturgeon migrate to the post-Libby Dam spawning reach (rkm 228.0-246.0) (Paragamian and Kruse, 2001; Paragamian et al., 2001). The males arrive first, followed by the females about a week later. This reach is comprised primarily of sand substrate, which is thought to be poor habitat for survival of eggs and larvae when compared with white sturgeon spawning habitat in the Columbia River (Parsley et al., 1993; McCabe and Tracy, 1994; Parsley and Beckman, 1994). More suitable spawning substrates of cobble and gravel begin at Bonners Ferry, extending upstream from rkm 244.6. Only a limited amount of spawning has taken place: 1991, 1992, and 2001 (Apperson and Wakkinen, 1992; Paragamian et al., in progress).

It is not known where Kootenai River white sturgeon spawned pre-Libby Dam or why white sturgeon spawn within the present reach of the river. It may be an evolutionary trait inherited over 10 000 years of segregation from other white sturgeon (Northcote, 1973). They may be compelled to spawn there because historic habitat is unavailable or because of false environmental cues. Recent measures to recover the wild population have shown no indication of improved stock densities, although hatchery releases of age 2+ white sturgeon have shown high survival (Ireland et al., this issue). The present spawning location appears to limit successful survival of eggs and larvae (Paragamian et al., 2001). To our knowledge, tagged white sturgeon have never moved upstream

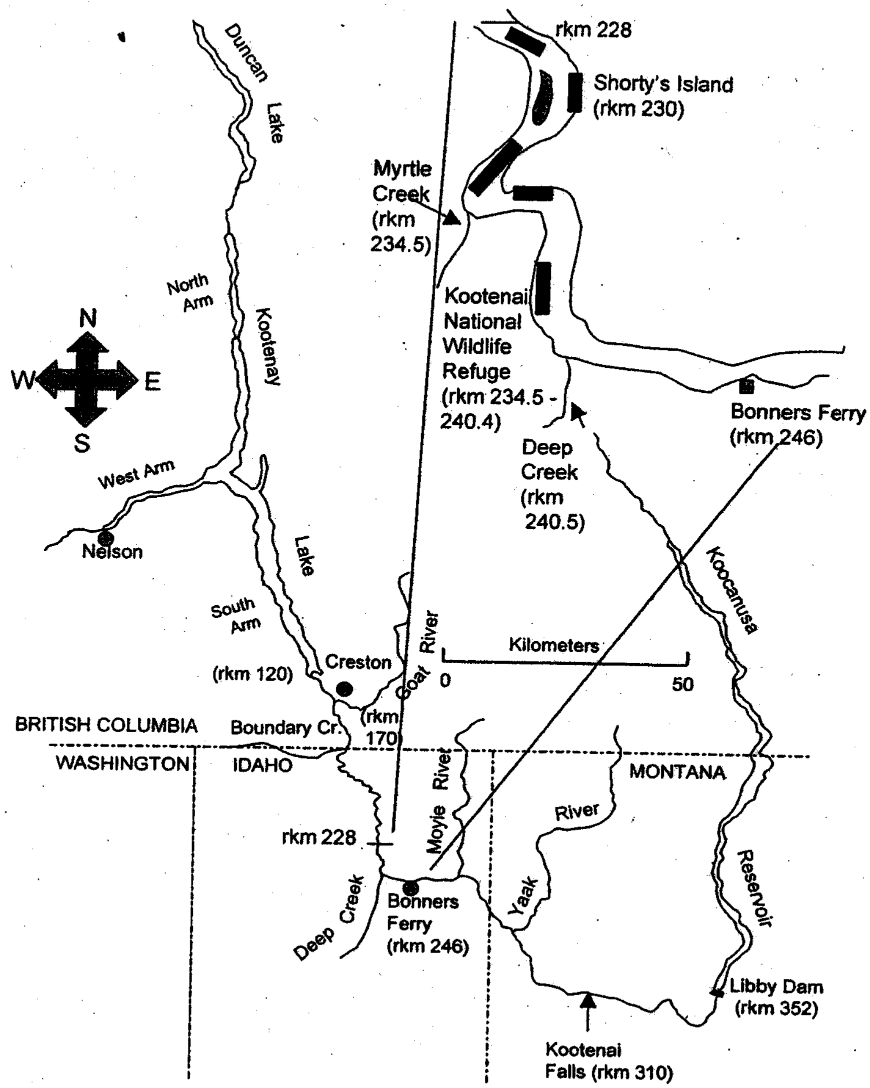

Fig. 1. Location of the Kootenai River, Kootenay Lake, Lake Koocanusa, Libby Dam, Bonners Ferry, and important points. Distances from the northernmost reach of Kootenay Lake are in river kilometers (rkm) and are indicated at important points. Main spawning locations are black rectangles

of Bonners Ferry and white sturgeon that have moved in the vicinity of the preferred substrate have stayed there for only a few days only to return downstream to the main body of spawners (Paragamian and Kruse, 2001). In addition, preliminary observations of adult white sturgeon movement suggest individuals are spawning in the lower reach of the river early in the spawning season and progressively moving upstream, never reaching the preferred habitat of gravel and cobble substrate above rkm 244.6. White sturgeon moving from one spawning location to another may be an additional activity that has been modified by the physical changes to the Kootenai River since the operation of Libby Dam began. The primary objective of this paper is to compare, within each spawning season and between seasons, the spatial and temporal pattern of egg collections (as an indicator of spawning location) and the spatial and temporal pattern of suspected spawners as determined by their movement.

Study Site

The Kootenai River is in the upper Columbia River basin. The river originates in Kootenay National Park, BC, flows south into Montana and turns northwest at the site of Libby Dam (Fig. I). As the river flows through the northeast corner of the Idaho panhandle it shifts to the north and enters Kootenay Lake, BC. The Kootenai River joins the Columbia River at Castlegar, BC. Our primary study reach was from rkm 228.0 to 247.0 (Fig. I). The spawning area. (Paragamian et al., 2001) was divided into three main sample reaches: lower from rkm 228.0 to 233.4, middle from rkm 233.5 to 239.9 and upper from rkm 240.0 to 247.0. The lower reach is the Shorty's Island area up to the downstream end of the first bend below Myrtle Creek and is comprised mostly of water 5-15 m in depth and sand/silt substrates (Fig. 1). The middle reach includes the Myrtle Creek confluence with the Kootenai River, several deeper pools, sand/silt substrates, and three river bends. The upper reach is comprised of along depositional zone (rkm 240.0-244.1) with a deep pool at rkm 244.5 (23 m deep) and gravel and cobble substrate within shallow water (2-4 m) from rim 244.6 to 247.0. To further define spawning locations, the lower and middle reaches were divided into six different geographic units based on white sturgeon spawning locations (capture of eggs) and telemetry contacts. These were: Lower Shorty's Island (rkm 228.0-229.5), Middle Shorty's Island (rkm 229.6-231.5), Upper Shorty's Island (rkm 231:6-233.4), Myrtle Creek (rkm 233.5-234.7), Wildlife Refuge (rkm 234.8-237.5), and

Deep Creek (rkm 237.6-240.5). Sampling was also performed outside these reaches, but no evidence of spawning was found (Paragamian et al., 2001).

Methods

White sturgeon sampling and telemetry

Our posteriori analytical design was to evaluate egg (spawning) locations and telemetry contacts with white sturgeon spawners over time and location in order to assess spawning and movement within each spawning season and between seasons. Up to seven late vitellogenic females and seven mature males were fitted with radio and sonic transmitters each year (1994-1999) (Paragamian and Kruse, 2001). Suspected spawners for the upcoming season were fitted with radio (50-month, Advanced Telemetry Systems, Isanti, MN) and ultrasonic transmitters (6-48-month, Sonotronics, Tucson, AZ) attached through the base of the dorsal fin. Location of each fish was recorded to the nearest 0. 1 km (Paragamian and Kruse, 2001). Spawner groups described in the text were concentrations of adult male and female white sturgeon with sonic or radio transmitters that were assumed to be engaged in spawning activities with other adults, and eggs were collected from the. general area.

White sturgeon egg collections, effort, and ages of eggs

We sampled the spawning reach annually from May to June for evidence of spawning (presence of eggs) with 75 to 100 artificial substrate mats (Paragamian et al., 2001), herein called mats, as described by McCabe and Beckman (1990). We assumed the capture of eggs by this method was evidence that white sturgeon spawned in the vicinity of their collection (Parsley et al., 1993; McCabe and Tracy, 1994; Parsley and Beckman, 1994). This sampling method is effective because white sturgeon are broadcast spawners and eggs are adhesive for only a short time, sinking immediately after expulsion (Stockley, 1981; Brannon, 1984; Cherr and Clark, 1985; Wang et al., 1985). Mat placement was designed to help identify white sturgeon spawning locations, including deployment within staging reaches of sturgeon. In 1994, mats were set every 0.5 km, from rkm 228.0 to rkm 245.6. In 1995, the mats were distributed from rkm 215.0 to rkm 246.0 to sample a variety of habitats, including three staging areas. In 1996, the mats were distributed primarily in the main channel from rkm 228.0 to rkm 247.7 [this was performed because after 5 years of sampling no eggs were ever collected near the river margins (Paragamian et al., 2001)]. From 1997 to 1999, mats were placed from rkm 227.0 through rkm 247.0 and a standardized sampling regime was implemented based on the location and density of adult fish (Paragamian et al., 1997). Mats were checked daily, and eggs were removed and stored in labeled vials containing formalin or alcohol solution. The capture of one or more eggs from a single mat was termed a collection. Estimated spawn date for eggs were determined by the method of Beer (1981) by staging each viable egg from various collection sites and then back-calculating to spawn date.

Data analysis

Our temporal analysis of egg collections focused on the sampling dates common to all 6 years (May 7-June 28) and the rkm locations where eggs were collected (rkm 228.0-239.9). Sampling date intervals would allow us to test for the presence of a temporal spawning, pattern as related to location. The entire sampling period was originally divided into eight date categories (variable date category =DATECAT) as follows: May 7-13, May 14-20, May 21-27, May 28-June 3, June 4-10, June 11-17, June 18-24, and June 25-28. The two date-categories at the beginning of the sampling period were later combined into a single 2-week date category, and the two categories at the end were combined into an 11-day category to account for the periods with low or no egg collection in one or more years. Divided this way, all date categories contained temperature and flow values that fell within one standard deviation of the mean as derived from the entire data set. This corresponded to a variation in temperature of $\pm$1.5 °C and a variation in flow of 140.7 m^3 s^{-1} in a given seven to 14-day period during which spawning could take place and over which our analysis covered (Paragamian et al., 2001). We used the number of collections with eggs present in our analysis. Thus, a sample of one egg or 100 was a single count. We did not use number of eggs or catch per unit effort because of the high variability in the collection of eggs on any one mat (Paragamian et al., 2001). A single mat could collect over 100 eggs if a female white sturgeon was spawning in close proximity, while a second mat nearby may collect only a few eggs or none.

For sampling location relative to rkm we used only the lower and middle reaches because no eggs were collected in the upper reach from 1994 to 1999 (variable river kilometer category = RKMCAT): (i) RKMCAT l - lower river reach, rkm 228.0-233.4 and (ii) RKMCAT 2 - middle river reach, rkm 233.5-239.9.

We used x^2 contingency analysis to examine whether the number of egg collections across date periods was evenly distributed in the lower and middle reaches for each year and across years. Conover (1980) suggests a row (r) by column (c) contingency table may be used to present a tabulation of data where each element may be classified in only one of r different categories according to one criterion and only one of c different categories according to a second criterion: The x^2 test procedure in STATISTIX (Analytical Software, 1998) is appropriate to analyze r x c tables of discrete data and to examine the hypothesis that the row-classifying variable (RKMCAT) acts independently of the column-classifying variable (DATECAT). It assumes non-negative count data and is reliable if the expected cell values fall within Snedecor and Cochran's (1989) guidelines for minimum expected values. These requirements were met by our data.

We examined movement of individual sturgeon and spawning groups between locations from which eggs were collected. These data provided circumstantial evidence of the presence of a tagged adult during at least one spawning event at a location from which eggs were collected for the years 1994 to 1999.

White sturgeon radio and sonic telemetry data for 1994-1999 were evaluated by using the same lower and middle reach and date categories (1-6, corresponding with the common sampling dates) as the analysis of egg collection locations. Counts of telemetry observations for fish expected to spawn within each rkm/date category combination were determined. We used x^2 contingency analysis to determine whether the number of telemetry observations for expected spawners in the lower (228.0-233.4) and middle (233.5-239.9) reaches were the same across all date periods. This analysis enables us to evaluate both the movement and egg collection data with respect to location and date. The analysis was run on each year independently for 1994-1999, and for 1994-1999

Table 1
Mat sampling effort in mat-days, catch, and catch-per-unit effort (eggs/mat-day) by twelve river kilometer sections for years 1994–1999

Rkm section	1994 Mat days	1994 No. eggs	1994 CPUE	1995 Mat days	1995 No. eggs	1995 CPUE	1996 Mat days	1996 No. eggs	1996 CPUE	1997 Mat days	1997 No. eggs	1997 CPUE	1998 Mat days	1998 No. eggs	1998 CPUE	1999 Mat days	1999 No. eggs	1999 CPUE
< 228.0				301.0	0	0												
228.0–229.5	422.2	42	0.099	574.1	13	0.023	236.9	0	0	406.5	0	0	590.8	39	0.066	548.1	19	0.035
229.6–231.5	490.4	133	0.271	627.1	62	0.099	37.9	0	0	391.9	0	0	482.8	173	0.358	388.2	144	0.371
231.6–233.4	3.0	0	0	124.0	0	0	419.1	52	0.124	388.0	1	0.003	410.9	0	0	371.8	0	0
233.5–234.7	8.9	0	0	115.0	71	0.617	233.5	30	0.128	545.1	11	0.020	458.6	14	0.031	466.6	0	0
234.8–237.5	356.9	38	0.106	600.1	16	0.027	756.9	262	0.346	666.3	33	0.049	697.0	55	0.079	616.1	21	0.034
237.6–240.5	367.7	0	0	151.0	0	0	144.0	0	0	513.8	30	0.058	401.1	112	0.279	388.3	0	0
240.6–243.9	329.3	0	0	124.1	0	0	194.7	0	0	358.1	0	0	255.5	0	0	308.9	0	0
244.0–244.6	163.2	0	0	177.0	0	0	340.5	0	0									
244.7–246.6	259.6	0	0	484.0	0	0	1840.5	0	0	804.7	0	0	304.8	0	0	173.3	0	0
246.7–247.7							244.4	0	0	181.1	0	0	157.4	0	0	125.4	0	0
> 247.7																		
Total	2401.3	213	0.089	3277.6	162	0.049	4448.3	349	0.078	4255.6	75	0.018	3758.8	393	0.105	3386.7	184	0.054

combined. As in the previous x^2 analysis of egg collection locations, the method assumes random sampling and that each observation may be classified in exactly one of r categories (RKMCAT) and only one of c categories (DATECAT) (Conover, 1980).

Results

The initiation of white sturgeon spawning occurred as early as May 6 in 1998 and as late as June 8 in 1996. The last date of egg collection was as early as June 12 in 1998 or as late as June 28 in 1999. A total of 213, 162, 349, 76, 393, and 184 eggs were collected from 1994 to 1999, respectively (Tables 1. and 2). Effort for the study reaches ranged from 3 mat-day for rkm 231.6-233.4 in 1994 (1 mat-day is a 24-h set) to 1840 mat-day for rkm 244.7-246.6 in 1996. The eggs mat-day $^{-1}$ of effort ranged from 0.003 in 1997 for rkm 231.6-233.4 to 0.617 eggs mat-day $^{-1}$ in 1999 for rkm 233.6--234.7, no eggs were collected in the upper reach.

We determined that there were five primary spawning locations for white sturgeon from 1994 to 1999, most in the vicinity of outside river bends (Fig. I). The five most important reaches where spawning predominantly occurred were rkm 228.7-229.6 (Lower Shorty's Island), rkm 230.0-231 (Middle Shorty's Island), rkm 235.2-235.9 (Kootenai National Wildlife Refuge), rkm 236.1-236.9 (Kootenai National Wildlife Refuge), and rkm 238.9-239.9 (Deep Creek).

Table 2
Number of white sturgeon eggs collected within river kilometer study sections, Kootenai River, Idaho (1994-1999)

River Section	Year 1994	1995	1996	1997	1998	1999	Total
<228.0	-	0	-	-	-	-	0
228.0-229.5	42	13	0	0	39	19	113
229.6-231:5	133	62	0	0	173	144	512
231.6-233.4	0	0	52	1	0	0	53
233.5-234.7	0	71	30	11	14	0	126
234.8-237.5	38	16	262	33	55	21	425
237.6-240.5	0	0	5	30	112	0	147
240.6-243.9	0	0	0	0	0	0	0
244.0-244.6	0	0	0	-	-	-	0
244.7-246.6	0	0	0	0	0	0	0
246.7-247.0	-	-	0	0	0	0	0
Total	213	162	349	75	393	184	

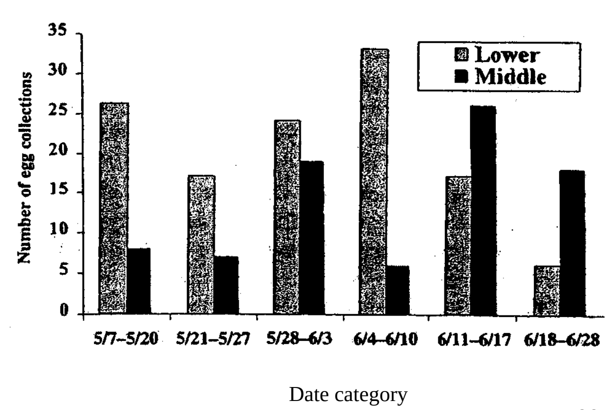

Fig. 2. Total number of egg collections by date category from 1994--1999 fog the lower and middle Kootenai River white sturgeon spawning reaches

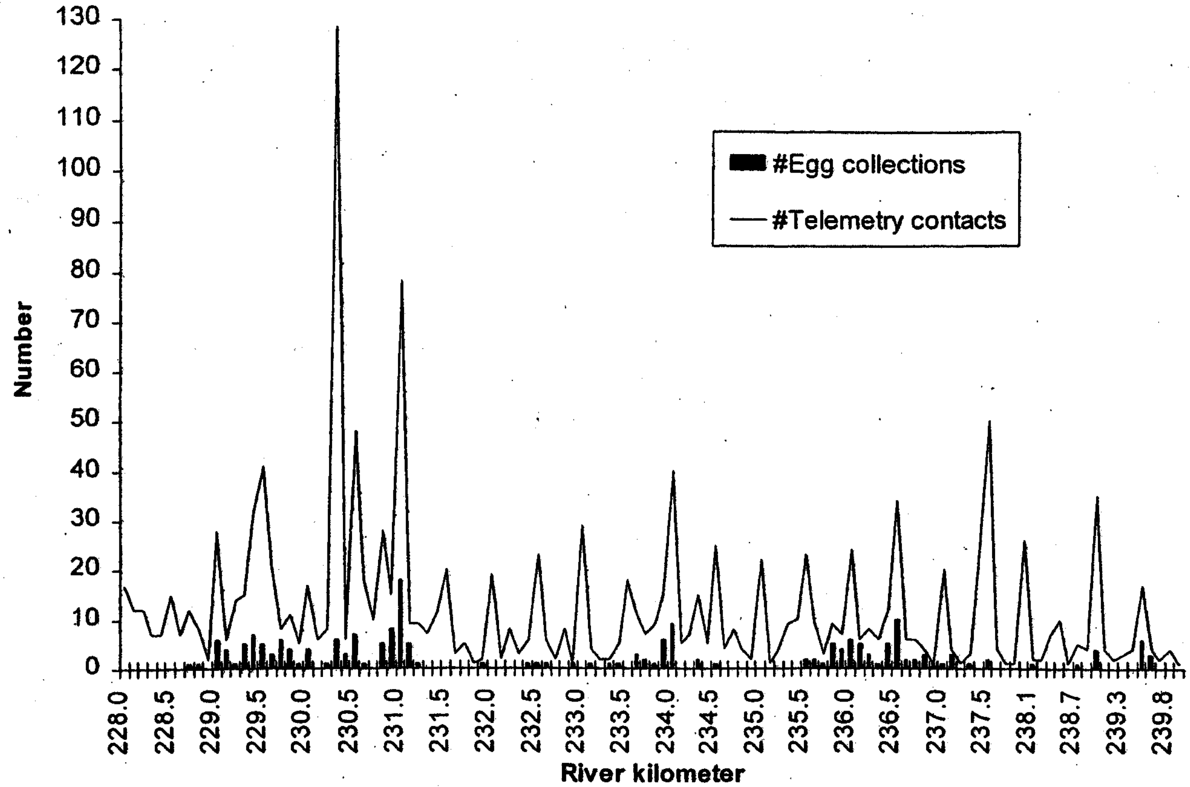

Fig. 3. Total number of egg collections and total number of telemetry contacts by river kilometer (rkm) in the Kootenai River, 1994-1999

Eggs were collected 207 different times from 1994 to 1999, 123 times in the tower reach and 84 times in the middle reach (Fig. 2). The average date for all collections in the lower reach was June 3, while in the middle reach it was June 6. The x^2 goodness-of-fit statistic was significant ($P < 0.0001$), indicating that the number of egg collections for 1994-1999 was different in the two reaches. These findings indicated that a temporal spawning pattern occurred, with spawning usually taking place first in the lower reach and last in the middle reach. For all date categories combined, 18% more egg collections occurred in the lower reach (rkm 228.0-233.4) than in the middle reach (rkm 233.5-239.9). Eggs were collected more often than expected from May 7-27 and June 4-10 in the lower reach. Outside of these date parameters, all showed higher than expected egg collections in the middle reach. The significance of the number of times eggs were collected from June 18-28 (58% less than expected in the lower reach and 85% more than expected in the middle reach) may be because of the number of egg collections occurring late in the season in 1996 and 1997. Thirty percent of the egg collections in 1996 and 36% in 1997 occurred after June 17, in contrast to 100% of the collections in 1995 and 1998 and 97% in 1994 occurring by June 17.

We monitored the movement of white sturgeon within six segments of the lower and middle reaches of the Kootenai River as previously described. A total of 1234 contacts with potential spawners were made during May and June for the years 1994-1999 (Fig. 3). Adults with transmitters were often only a few meters apart. The movement of individual sturgeon and spawner groups to different locations from which eggs were collected was summarized (Table 3). Some adults were recorded at as many as four locations from which eggs were collected and on the date eggs were estimated to have been released. Based on the frequency of contacts, adult white sturgeon appeared to utilize at least four important locations: rkm 228.7-229.5 (Lower Shorty's island), rkm 230.0-231 (Middle Shorty's Island), rkm 235.2-235.9 (Kootenai National Wildlife Refuge), and rkm 236.1-236.9 (Kootenai National Wildlife Refuge), and to a lesser extent, two others.

All of the x^2 goodness-of-fit statistics for analysis of the count of telemetry contacts with white sturgeon by reach and date category were significant, with the exception of 1999 (Tables 4 and 5). That is, for all years independently, 1994-1998, and for the combined years 1994-1999, the data suggests that the numbers of telemetry contacts of expected spawners in the lower and middle reaches were different across date categories for the period May 7-June 28. There were greater than expected numbers of telemetry contacts with spawners during date category one (May 7-20) within the lower reach (rkm 228.0-233.4) in 4 of 6 years (1994, 1995, 1996, and 1999). Greater than expected numbers of movements were also made to the lower reach during the latest date category (June 18-28) in 4 of 6 years (1994, 1995, 1996 and 1997). Movements by spawners into the middle reach (rkm 233.5-239.9) were observed more often than expected during date categories two (May 21-27) and three (May 28-June 3) in 5 of 6 years (1994, 1995, 1996, 1997, 1999 and 1994, 1995, 1997, 1998, 1999, respectively). This was also true during date categories four (June 4-10) and five (June 11-17) in 3 of 5 years (1995, 1997, 1998 and 1994, 1996, 1997, respectively).

The results of the white sturgeon movement data analysis are similar to the results of the egg collection data analysis. The number of telemetry contacts in a given reach, just like the number of egg collections, was temporally distributed. In the egg collection analysis, there were 18% more egg collections in the lower reach than in the middle reach for

Table 3 . Estimated spawn dates and locations of groups of white sturgeon spawners within six geographic reaches of the Kootenai River 1994-1999. Each year individual male (M) and female (F) spawners assigned a consecutive number

	1994		1995		1996		1997		1998		1999	
Spawning Location	Estimated Spawn date	Adults	Estimated Spawn date	Adults	Estimated Spawn date	Adults	Estimated Spawn date	Adults	Estimated Spawn date	Adults	Estimated Spawn date	Adults
Lower Shorty's (rkm 227-229.5)	May 22, . 24, 25, 27 June 2, 3, 4	M1 Fl, F2, F3	May 23, 24, June 1, 5, 13	M1 Fl, F2, F3	None	None	None	None	May 6, 7, 10, 11, 12, 13, 24, 25, 26, 27, 28, 29, 30 June 2	M1, M2, M3, M4, M5, M6, M7 F1, F2 F3, F4, F5	May 30, 31 June 1, 2, 7, 8, 15, 16,	M1, M2, M3, M4, M5 F1, F2, F3, F4
Middle Shorty's (rkm 229.6-231.5	None	None	May 27, 28, 29, 30, 31 June 1, 2, 4, 6, 7, 13	M1, M2, M3 Fl, F2, F3, F4, F5, F6	None	None	None	None	None	None	June 1, 7	M6, M4
Upper Shorty's (rkm 231.6-233.4)	May 14, 15, 16, June 2, 3, 4, 10	M2, M3, M4 F3, F4, F5, F6	None	None	June 8 9, 10, 12	M1, M2, M3, M4, M5, M6 F1, F2, F3	June 11	M1	None	None	None	None
Myrtle Creek (rkm 233.5-234.7)	May 13, 14, 15, 16	M1	May 28, 30 June 1, 2. 13	M2, M3, M4 F2, F4, F6, F7	June 6, 7, 8, 9, 10	M1, M2 M3, M4, M5, M6, M7 F1, F4, F5, F6	June 11, 12, 13, 14	M1, M2	May 11, 24, 30 June 2, 5	M3, M7, M8 F3	None	None
Wildlife Refuge (rkm 234.8-237.5)	None	None	June 6, 13	M3, M4 F2, F4, F5, F6, F8, F9	June 9, 10 11, 12, 13, 14, 15, 16, 18, 19, 20, 21, 22, 23, 24	M1, M2 M3, M4, M6, M7 Fl, F2, F3, FS, F6, F7	June 9, 10, 11, 12, 20, 21	M1, M3 Fl, F2, F3	May 27, 28, 29, 30 June 3, 4, 5	M5, M6 M7, M9 F6	May 31 June 1, 16, 19	F1, F5
Deep Creek (rkm 237.6-240.5)	None	None	None	None	June 13, 14, 16	M1, M4, M5, M7 F3, F4, F5, F6	June 10, 13	M3 M4, M5, M6 F2	May 11, 12, 13, 22, 23, 24, 25, 26	M5, M6, M7, M8, M9 F6	None	None

Table 4
x^2 tests of telemetry location data, 1994-1999, to determine differences by time and location

Year	x^2 Statistic	d.f.	P-value
1994	18.01	5	0.0029
1995	30.88	5	0.0000
1996	20.57	5	0.0010
1997	33.51	5	0.0000
1998	10.63	5	0.0591
1999	5.13	5	0.4001
1994-1999	20.14	5	0.0012

the period 1994-1999. For the same period, there were 12.5% more spawner movements to the middle reach than to the lower reach.

Discussion

The temporal pattern of individual sturgeon shifting spawning location within the same season, over a 10-km reach of river with sand substrate, appears to be unique to the Kootenai River population of white sturgeon. Although there are several examples in the literature of a sturgeon spawning reach similar in length to that of Kootenai River (Zakharyan, 1992), to our knowledge there are no reports of individual fish movement within a spawning reach.

Our study indicated each year that Kootenai River white sturgeon maintained a relatively consistent pattern in changing spawning locations. Spawning usually begins in the lower portion of the spawning reach during early to mid-May. As the season progressed, spawning took place further upstream (the middle reach), extending about 10 km. Several spawning locations were consistently used over the 6-year study. In general, eggs were collected in locations and dates where we had telemetry contacts with suspected spawning white sturgeon. Likewise, we had telemetry contacts with suspected spawners where we collected eggs. However, there were occasions when egg collections did not occur where we had telemetry contacts. We attributed this difference to the mobility of white sturgeon. Our telemetry contacts were generally when white sturgeon were in spawning locations, but there is the probability that some sturgeon were in transition from one spawning location to another or had completed spawning. For this reason, the collection of eggs may be a better indicator of spawning location than adult locations alone.

Unlike Kootenai River white sturgeon, many sturgeon populations appear to spawn in specific locations; in some cases the sites are very limited in area. In contrast to our findings, Hildebrand et al. (1999) reported that a population of white sturgeon in the upper Columbia River, BC, consistently spawned in the same short reach of river, at the confluence of the Pend Oreille River (a dam is located upstream on the Pend Oreille River). This reach was used regardless of flaw and temperature; white sturgeon made a downstream migration to reach the spawning site, from what appeared to be potential gravel and cobble spawning habitat. Schaffter (1997), using artificial substrate mats and telemetry, found three spawning locations of white sturgeon in the Sacramento River, California, during 2 years of study, but did not report movement of individual sturgeon between sites. Sulak and Clugston (1999) noted Gulf sturgeon A. *oxyrinchus desotoi* spawned at three known sites, each as small as 9375 m^2 in tire Suwannee River, Florida. Fox et at. (2000) used telemetry and collected eggs of Gulf sturgeon in the Choctawatchee River, Alabama-Florida, and within the same year found six discrete spawning locations. Fox et at. (2000) made no reference to individual fish moving between sites within the 6 days of recorded spawning. Lake sturgeon *A. fulvescens* are also known to consistently spawn in specific locations. In the Sturgeon River, Michigan, lake sturgeon spawn within two rapids 0.11 and 2.11 km downstream of a hydroelectric dam (Auer, 1996). In the L'Assumption River, Quebec, lake sturgeon are known to spawn within several rapids (LaHaye et at., 1992)_ Votinov and Kas'yanov (1978) described the spawning reach of Siberian sturgeon *A. baerii* as a small section.

Many populations of sturgeon are fragmented and may be constrained to spawning in specific locations because of man-made barriers such as dams. The present spawning location of white sturgeon in the Kootenai River is 114 km downstream of Libby Dam, yet sturgeon are free to move further upstream. Thus, because the movement of the populations below dams is restricted they may not be good examples to compare with the Kootenai River white sturgeon (Parsley et al., 1993; McCabe and Tracy, 1994; Parsley and Beckman, 1994; Parsley and Kappenman, 2000).

Changing river velocities in the Kootenai River during the white sturgeon spawning season may be confusing, triggering a relocation response by sturgeon. The Kootenai River is a regulated river, but the mitigated spawning flows are only about 60%. of pre-dam spring discharge at Bonners Ferry and velocities at spawning locations are usually less than 1 m s^{-1} (Paragamian et al., 2001). Parsley (1991) indicated inadequate river velocities may limit the spawning of white sturgeon in the Columbia River. Parsley et .al. (1993) suggested white sturgeon key on high current velocities for spawning, and that coarse substrates are the result of the sorting of particles by higher velocities. Buckley and Kynard (19$2) indicated that water velocity and depth may be more important to spawning shortnose sturgeon than depth alone. If sturgeon are searching for specific velocities for a spawning cue, then they may be finding them in a reach of the Kootenai River with unsuitable spawning substrates. This may explain why statistical analysis of velocities at different egg collection locations

Table 5
Yearly occurrence of greater than expected movements by spawners to the lower and middle river reaches during the period 1994-1999

	Date					
	1	2	3	4	5	6
River reach	May 7-20	May 21-27	May 28-June 3	June 4-10	June 11-17	June 18-28
Lower (228.0-233.4)	`94,`95,`96`99	`98	`96	`94,96, '99	`95,`98,'99	`94,`95,`96,'97
Middle (233.5-239.9)	`97,`98	`94,`95,`96,'97,`99	`94,95,`97,`98,'99	`95,'97,`98	`94; 96,'97	'98,'99

in the Kootenai River from 1994-1997 showed that there were no differences in velocities between locations and years (Paragamian et at., 1997). The substrate at each location was sand.

Preliminary study suggests that the lower post-Libby Dam elevations of Kootenay Lake may be a factor affecting river velocities and white sturgeon spawning location (Duke et al., 1999). The Kootenai River downstream of Bonners Ferry is low gradient, and changes in Kootenay Lake elevation can be noticed as far upstream as Bonners Ferry. Lowering of Kootenay Lake, at the closing of Libby Dam, was a. unilateral decision by a Canadian utility and did not violate any International Joint Commission rulings (Duke et al., 1999). The historic elevation of Kootenay Lake prior to Libby Dam averaged 534.87 m, while after 1972 it averaged 532.68 m. We hypothesized that as Kootenay Lake rises, it has a backwater effect that changes river velocities and progressively compels white sturgeon to move further upstream to preferred velocities. Thus, suitable spawning and rearing locations are never reached because Kootenay Lake does not reach its former natural peak elevation. Furthermore, egg collection locations appeared to be related to lake elevation (Duke et al., 1999). This aspect of habitat change is under further analysis by the senior author. Recent studies of white sturgeon in the Upper Arrow Lake, BC, a natural lake on the Columbia River and impounded by a dam, suggest the same phenomenon may be occurring (L. Hildebrand, R. L. and L. Environmental Services Limited, Castlegar, BC, pers. comm.). The pre-dam spawning location of white sturgeon is unknown, but recent telemetry and egg collection results indicate they are now spawning in the upper transition reach of the lake and river.

The combination of what appears to be unusual movement by white sturgeon in the Kootenai River during the spawning season and spawning in what is thought to be unsuitable habitat (Paragamian et al., 2001) may be attributing to the Iailure of egg and larval survival and year-class recruitment. If this is the case, then present measures to recover the population may be inadequate. Further study is necessary to determine why white sturgeon move as they do, and a search for a likely historic spawning location should be pursued. If the historic spawning reach cannot be determined or eventually rehabilitated, then consideration should be given to habitat enhancement measures (Paragamian et al., 2001) at the major locations in the Kootenai River where adult white sturgeon are now spawning.

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