

Ovarian Fluid Pheromone Testing

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Table of Contents

List of Figures.....	iv
List of Tables	v
Objective.....	2
Methods	3
Results.....	5
Experiment 1.....	6
Experiment 2.....	12
Discussion	14

List of Figures

Figure 1. Snapshot of northern pikeminnow (<i>Ptychocheilus oregonensis</i>) captured approximately 20 minutes after the start of experiment 1, trial 1.....	7
Figure 2. Snapshot of a suspected white sturgeon in center of frame; unfortunately water clarity makes it difficult to identify the fish at distance.....	7
Figure 3. Snapshot captured at the end of Experiment 1 Trial 1 containing two northern pikeminnow.	8
Figure 4. Snout and barbell of a white sturgeon are clearly identified in the top right corner of the video frame 2 minutes and 25 seconds after trial 2 initiated.....	11
Figure 5. A white sturgeon briefly crosses the upper left corner of the video frame at 13:53:52, or 5 minutes and 27 seconds after the start of trial 2.....	11
Figure 6. A white sturgeon briefly holds its position downstream of the pheromone nozzle at 13:58:38, or 10 minutes and 13 seconds after the start of trial 2.	12
Figure 7. Northern pikeminnow aggressively feeding from the pheromone nozzle during experiment 1 trial 2.....	12

List of Tables

Table 1. Summary of white sturgeon (WSG) radio detections and underwater video footage identifications during experiment 1 trial 1.....	9
Table 2. Summary of white sturgeon (WSG) radio detections and underwater video footage identifications during experiment 1 trial 2.....	10
Table 3. Summary of white sturgeon (WSG) radio detections and underwater video footage identifications during experiment 2 trial 1.....	13

Introduction and background

Chemoreception has been known widespread in the animal kingdom. The insects represent the most extensively studied examples of chemoreception in the animal kingdom (Carde, 1990; Chapman, 2000), and scientific research on the theme of chemical communication mediating various behaviors has led to the development of economically and ecologically important tools for the management of insect species of interest. In fish, pheromone-mediated behaviors, reproductive behaviors in particular, have been well documented (Liley and Stacey, 1983) but little information on the chemical identity of pheromones involved is available, except for a few studies where the chemical identity of the chemosensory cues was elucidated in goldfish (Sorensen and Stacey, 1999), catfish (Resink et al., 1989), and sea lamprey (Li et al., 1995; Li et al., 2002; Sorensen et al., 2005).

Chemical communication systems mediated by pheromones in the various animal groups have been offering useful biological tools in manipulating populations of interest (Carde, 1990; Li et al., 2003). The basic characteristics of pheromones, species-specificity and low threshold for responses, make them very useful in applying to fisheries management, once they are identified. In particular, better understanding of pheromone identities involved in critical life history stages could offer a possible target for population manipulation. In fisheries management pheromones could elicit significant physiological and behavioral responses in fish.

Ample evidence exists to support the notion that sturgeons heavily rely on their chemosensory system for feeding behaviors, homing, and male-female interactions (Bruch and Binkowski, 2002; Dadswell, 1979; Kasumyan, 1993, 1999; 2002; Kynard and Horgan, 2002). Chemical communication in sturgeons has been described in European species and some Atlantic coast species. In the earlier works by Kasumyan (1993, 1999), it was demonstrated that males are attracted by female postovulatory pheromones. In Russian sturgeon *A. gueldenstaedti* and starred sturgeon, *A. stellatus*, the odor of ovarian fluid from ovulatory females was found to be a highly effective stimulant for male sturgeons, demonstrating presence of chemical communication mechanisms mediated by sex pheromones (Kasumyan, 1993, 1999). It was also demonstrated in the shortnose sturgeons, *A. brevirostrum* that males can discover mature females by the odor (Kynard and Horgan,

2002). Field observations on white sturgeon in the spawning grounds showed that spawning activity begins after females move on to the site and begin ovulating, which indicates initiation of male spawning behaviors triggered by unknown chemical cues from ovulatory females (Bruch and Binkowski, 2002).

Stocking, habitat protection, and habitat restoration are the focus of recovery efforts in the Nechako River. In particular, xxx has been working to create suitable gravel substrate for spawning. However, there is a need to draw spawning adults to the spawning ground to make such habitat restoration efforts complete. Based on biological information from other sturgeon species, it can be speculated that white sturgeon also use chemical cues for their behavioral interactions during migration and reproduction. A better understanding of chemosensory mechanisms mediated by chemical cues could offer managers a scientific background for the formulation of the most efficient white sturgeon restoration strategies in the Nechako River. In this project, it was proposed to examine whether male sturgeons would display attractive behavior to female ovarian fluid in the natural environment.

Objective

To test the hypothesis that ovarian fluid can act as an attractant to mature adult white sturgeon in a river environment.

Methods

1. Ovarian fluid collection

Ovarian fluid was collected from Nechako White Sturgeon Conservation Hatchery wild brood stock. Ovulation was induced by double injection of GnRH on May 25 – 26 and on May 31 – June 1, 2015, which is typical timing of wild spawning activity in Nechako River. Ovarian fluid was stored for less than 24 hrs in -20 °C.

2. Application of ovarian fluid and tracking of white sturgeon

Ovarian fluid was dosed into Nechako River at strategic locations, during a time when white sturgeon (*Acipenser transmontanus*) spawning activity is typically observed. Prior to dosing the river, the technical working group searched the Nechako River spawning reach for radio-tagged white sturgeon using Lotek SRX800 mobile receiver. Time, location, radio frequency, maximum signal strength, and radio code were recorded for each unique fish detected in the area. If a radio code was detected multiple times, but within 30 seconds of a previous detection it was only recorded once and a running tally of minutes detected was recorded. If a radio code was detected once, and then the same code was detected more than 30 seconds after the previous detection it was recorded as a new detection.

Ovarian fluid dosing occurred in areas that were approximately 200 m upstream of radio tagged fish detections. The fluid was pumped into the river using a Masterplex peristaltic pump (Cole-Parmer, Vernon Hills, IL, USA) calibrated for ovarian fluid in the laboratory, using approximately 15 m of tubing, and a benthic mooring. Tubing of approximately 4 mm I.D. was used to ensure that some eggs present in ovarian fluid did not block the flow of ovarian fluid. The delivery/nozzle tubing was attached to the mooring approximately 1 m above the foot of the mooring using a combination of metal hose clamps and duct tape. Video recordings were collected using Shark Marine underwater camera, and recorded to MiniHD tapes using Canon Vixia HV30 (Canon, Japan). Tape footage was digitized using (NAME OF SOFTWARE) software.

Experiment 1

During the first trial of experiment 1 ovarian fluid flow rate was held constant at 20 ml/min. During the second trial of experiment 1 the ovarian fluid flow rate was modified to 100 ml/min for the first three minutes, and then down-regulated to 20 ml/min for the

remainder of the fluid. Trial 1 ovarian fluid dosing commenced at 13:09:05 on May 27th 2015, and ended at 13:39:17, for a total duration of 30 minutes and 12 seconds, and total ovarian fluid dose of 603 ml. Trial 2 (Table 2) of experiment 1 started at 13:48:25 in the same location as trial 1 and lasted for a total duration of 16 minutes and 37 seconds, and a total ovarian fluid volume of 572.4 ml.

Table 1. Summary of doses used the present pheromone study

Experiment	Doses and application duration	Locations and conditions
Exp 1 Trial 1	20 ml/min	0436351 easting, 5986881 northing, zone 10 river width = 143m, depth = 3.8m
Exp 1 Trial 2	100 ml/min for 3 mins, 20 ml/min for the rest of experiment	
Exp 2 Trial 1	100 ml/min for 5 min, 25 ml/min for 40 min	0433657 easting, 5986944northing, zone 10, River width = 145m, depth = 3.1m
Exp 2 Trial 2	200 ml/min for 5 min, no further release	

Experiment 2

A second experiment was carried out on June 2, 2015. It replicated the first experiment except the dosing rate was increased to test a hypothesis that greater concentration would result in increased white sturgeon attractiveness. Experiment 2 also consisted of two trials meant to retest the objective hypothesis using faster ovarian fluid flow rates, thus slightly more concentrated dosing. Experiment 2 occurred at a predetermined location just upstream of an 18-receiver VPS array used for precisely locating acoustically tagged fish. The dosing location was chosen for two reasons; 1) because it was within a known spawning location for white sturgeon, and 2) because of the possibility of attracting an acoustically tagged white sturgeon, in which case the VPS would collect detailed movement data of the attraction process. During the first trial of experiment 2 ovarian fluid flow rate started at 100 ml/min for the first 5 minutes, and then reduced to 25 ml/min for 40 minutes. During trial 2 ovarian fluid flow rate started at 200 ml/min for 5 minutes, and then no more ovarian fluid was pumped for the remaining 25 minutes of the trial. Experiment 2, trial 1 started on June 2nd, 2015 at 17:22:19. Trial 2 began at 18:04:36.

Biological data and spawning likelihood are provided for radio tagged fish detected during the experiment. Fish were considered spawners if they had been tagged in 2015 and their gonads were mature, or if they had been captured and tagged in 2014 and their gonads were near maturity. Fish were considered possible spawners if they had been captured and tagged previous to 2014, and they were large enough to be considered mature adults. Fish were considered unlikely spawners if they had been captured and tagged in 2015 and their gonads were not mature, or if they had been captured and tagged in 2014 and their gonads were mature and ready to spawn in 2014.

3. Data analysis

River discharge data for the days of experiments were obtained from Canada water office (https://wateroffice.ec.gc.ca/report/report_e.html?mode=Graph&type=realTime&stn=08JC001&dataType=Real-Time&startDate=2015-06-01&endDate=2015-06-06&prm1=47&y1Max=&y1Min=&prm2=5&y2Max=&y2Min=)).

Results

River Flow Conditions and Dilution Factor

During the experiments, water discharge at the experimental sites was approximately 675 m³/s. Assuming ovarian fluid applied to the river become totally mixed with river water, dilution factors for each dose can be estimated. At 20 ml/min, 100 ml/min, and 200 ml/min doses, it was estimated that dilutions factors were 2.25×10^9 , 400×10^6 , and 200×10^6 , respectively.

Experiment 1

Experiment 1 was conducted on May 27th, 2015, and consisted of two experimental trials. Five radio tagged white sturgeon were detected between river kilometer (rkm) 130 and 135 (Table 1), and two of those fish were located relatively close together (~200 m separation). Due to the presence of two fish relatively close together, the technical working group moved upstream, just out of detection range of those two fish (codes 42 and 38) for experiment 1 dosing location (Figure 1).

Three unique radio codes were detected between 13:16:00 and 13:18:00, however these radio code detections were low signal strength. Code 64 was detected for less than a minute, code 15 was detected for one minute, and code 18 was detected for just over two minutes. Code 13 was detected pre-dosing, and remained within the detection range for nearly the entire dosing period of trial 1. Code 13 was typically low signal strength thus relatively far from the dosing location, however that fish appeared to move close to the dosing location at 13:28:08 (92 signal strength) and at 13:35:26 (131 signal strength).

Before reporting underwater video results, it should be noted that water clarity was extremely low making it difficult to identify fish more than an estimated 0.5 m away from the lens. In addition it was also difficult to extract snapshots of clearly identifiable fish, but when watching the video in motion there are certainly instances of fish moving within frame. Underwater video footage revealed a small, unidentifiable fish present in frame at 13:25:25. At 13:25:54 the snout of a large fish (suspected white sturgeon) enters the top left frame of the video, but water clarity prevents a 100% certain identification. At 13:26:25 another white sturgeon-shaped fish moves from left to right across the video frame, and again from right to left across the frame at 13:26:42. A northern pikeminnow (*Ptychocheilus oregonensis*) enters the frame at 13:29:12 (Figure 2), and repeatedly enters the video frame inspecting the pheromone nozzle until 13:29:34.



Figure 1. Snapshot of northern pikeminnow (*Ptychocheilus oregonensis*) captured approximately 20 minutes after the start of experiment 1, trial 1.

A northern pikeminnow is identified within frame again at 13:30:09, and continues to come in and out of frame until 13:33:25. At 13:34:00 a relatively large fish with a white outline along the ventral edge of the body moves from the top of the frame towards the bottom and slightly towards the right edge of the frame. A scute row is not clearly visible, but this is another suspected white sturgeon captured on frame. A similar shape appears on frame at 13:34:36 (Figure 3), but the fish is too far away to clearly identify.



Figure 2. Snapshot of a suspected white sturgeon in center of frame; unfortunately water clarity makes it difficult to identify the fish at distance.

Northern pikeminnow continue to enter and exit the video frame for the remainder of the experiment. At 13:35:25 two pikeminnow are seen within frame (Figure 4).



Figure 3. Snapshot captured at the end of Experiment 1 Trial 1 containing two northern pikeminnow.

Table 2. Summary of white sturgeon (WSG) radio detections and underwater video footage identifications during experiment 1 trial 1

Experiment 1 - Radio and Video Tracking Summary					
Time (24hr)	Radio Freq.	Radio Code	Power	Duration (min)	Comments
<i>Predose</i>					
11:51:00	149.52	62	50	NA	Male, unlikely spawner, 206.2 cm TL, 2015-04 release
11:54:00	149.52	65	97	NA	Male, possible spawner, 174.4 cm TL, 2012-10 release
11:57:00	148.6	32	94	NA	Female, spawner, 272.5 cm TL, 2015-05 release
12:05:00	149.52	42	109	NA	Male, possible spawner, 248.4 cm TL, 2014-05 release
12:06:00	149.52	38	104	NA	Female, unlikely spawner, 236 cm TL, 2015-05 release
13:05:00	149.52	13	<50	35	Male, possible spawner, 202.4 cm TL, 2011-05 release
<i>Trial 1 - Start at 13:09:05</i>					
13:16:15	149.52	64	<50	<1	Female, possible spawner, 213.8 cm TL, 2012-10 release
13:16:15	149.52	15	<50	1	Male, possible spawner 218.1 cm TL, 2011-04 release
13:17:50	149.52	18	<50	2	Male, possible spawner, 275 cm TL, 2011-04 release
13:25:25	NA	NA	NA	<1	Small unidentifiable fish in video frame for a couple seconds
13:25:54	NA	NA	NA	<1	Snout of large fish (suspected WSG) briefly in frame
13:26:25	NA	NA	NA	<1	Suspected WSG
13:26:42	NA	NA	NA	<1	Suspected WSG
13:28:08	149.52	13	92	35	Male, possible spawner, 202.4 cm TL, 2011-05 release
13:29:12	NA	NA	NA	<1	NPM inspects/feeds at pheromone release nozzle
13:30:09	NA	NA	NA	3	NPM intermittantly inspects/feeds at pheromone release nozzle
13:34:00	NA	NA	NA	1	Suspected WSG
13:35:25	NA	NA	NA	<1	Two NPM in frame
13:35:26	149.52	13	131	35	Male, possible spawner, 202.4 cm TL, 2011-05 release

NPM = Northern pikeminnow ; WSG = white sturgeon

Code 18 was detected at 13:53:02, for just over three minutes and peak signal strength of 64, then two unique fish (codes 44 and 16) were detected at 13:54:50 and 13:55:20 respectively, for less than one minute. Code 15 was detected at 14:03:25, just prior to the end of trial 2 at 14:05:02.

Table 3. Summary of white sturgeon (WSG) radio detections and underwater video footage identifications during experiment 1 trial 2.

Experiment 1 - Radio and Video Tracking Summary					
Time (24hr)	Radio Freq	Radio Code	Power	Duration (min)	Comments
<i>Trial 2 - Start at 13:48:25</i>					
13:50:12	NA	NA	NA	<1	NPM intermittantly inspects/feeds at pheromone release nozzle
13:50:45	NA	NA	NA	<1	Suspected WSG
13:50:50	NA	NA	NA	<1	WSG clearly identified; only in frame for a second
13:51:04	NA	NA	NA	<1	NPM briefly enters frame
13:53:02	149.52	18	64	3	Male, possible spawner, 275 cm TL, 2011-04 release
13:53:52	NA	NA	NA	<1	WSG briefly crosses upper right corner of video frame
13:54:50	149.52	44	<50	<1	Male, unlikely spawner, 243.8 cm TL, 2014-05 release
13:55:20	149.52	16	<50	<1	Female, possible spawner, 221.1 cm TL, 2011-05 release
13:55:53	NA	NA	NA	<1	NPM briefly enters frame
13:58:38	NA	NA	NA	<1	WSG briefly holds position downstream of nozzle
14:01:30	NA	NA	NA	<1	NPM aggressively feeds from nozzle
14:03:25	149.52	15	<50	1	Male, possible spawner, 218.1 cm TL, 2011-04 release

NPM = Northern pikeminnow ; WSG = white sturgeon

During the first three minutes of trial two's video footage the ovarian fluid was relatively obvious when discharging from the nozzle, as one might expect at a flow rate 5x higher than trial 1. One northern pikeminnow entered the video frame at 13:50:12 and continued to enter and exit the frame for 10 seconds. At 13:50:45 a large fish (suspected

white sturgeon) briefly crosses the top right corner of the video frame, and then at 13:50:50 a white sturgeon can be clearly identified in the top right corner of the video frame (Figure 5).



Figure 4. Snout and barbell of a white sturgeon are clearly identified in the top right corner of the video frame 2 minutes and 25 seconds after trial 2 initiated.

A pikeminnow enters the video frame and inspects the nozzle at 13:51:04 for several seconds. At 13:53:52 a white sturgeon briefly crosses the upper left corner of the video frame (Figure 6).



Figure 5. A white sturgeon briefly crosses the upper left corner of the video frame at 13:53:52, or 5 minutes and 27 seconds after the start of trial 2.

A pikeminnow inspects the nozzle at 13:55:53. A white sturgeon once again enters the video frame at 13:58:38, and holds its position very briefly in the center of the video frame just downstream of the nozzle (Figure 7).



Figure 6. A white sturgeon briefly holds its position downstream of the pheromone nozzle at 13:58:38, or 10 minutes and 13 seconds after the start of trial 2.

At 14:01:30 a pikeminnow aggressively feeds from the nozzle, making direct contact with its mouth (Figure 8).



Figure 7. Northern pikeminnow aggressively feeding from the pheromone nozzle during experiment 1 trial 2.

Experiment 2

The pump was inactive between 17:27:22 and 17:28:02 due to switching the flow rate on the pump control interface. Seven unique white sturgeon were detected between 17:29:12 and 17:45:10, but all for short durations and very low power (less than a minute; see table 3).

Trial 2 consisted of one large dose of ovarian fluid, and then passive telemetry to monitor subsequent activity. No radio tagged fish were detected after the single large dose of ovarian fluid. No fish were captured on underwater video during experiment 2

Table 4. Summary of white sturgeon (WSG) radio detections and underwater video footage identifications during experiment 2 trial 1.

Experiment 2 - Radio and Video Tracking Summary					
Time (24hr)	Radio Freq	Radio Code	Power	Duration (min)	Comments
<i>Trial 1 - Start at 17:22:19</i>					
17:29:13	148.6	15	<50	<1	Female, unlikely spawner, 250 cm TL, 2014-05 release
17:29:13	148.6	44	<50	<1	No database record
17:29:13	148.6	30	54	<1	Female, spawner, 238 cm TL, 2015-05 release
17:29:14	148.6	24	<50	<1	Male, unlikely spawner, 227.4 cm TL, 2014-05 release
17:29:14	148.6	34	<50	<1	Female, spawner, 252.5 cm TL, 2015-05 release
17:30:06	148.6	18	<50	<1	Male, unlikely spawner, 245 cm TL, 2014-05 release
17:32:06	148.6	23	<50	<1	Male, spawner, 241.2 cm TL, 2014-05 release
17:45:10	148.6	58	<50	<1	No database record

NPM = Northern pikeminnow ; WSG = white sturgeon

Discussion

During Experiment 1 trial 1 a total of 4 unique radio tags were detected and 4 events of suspected white sturgeon came within video frame. Only one radio tag detection reached a signal strength above 100 indicating only that radio tagged fish (code 13) swam relatively close to the pheromone release location; the other radio tags were not homing into the exact pheromone release location. Despite low power signals on most of the radio detections, the fact that new tags entered the detection zone as short as 7 min and 10 sec after releasing ovarian fluid suggests radio tagged sturgeon were attracted towards the release location. Perhaps the concentration or flow-rate of the ovarian fluid (20ml/min during trial 1) release was too small to allow sturgeon to pinpoint the release location. Most radio tag detections were also very brief (typically less than one minute) suggesting the tagged fish quickly became disinterested in locating the source of ovarian fluid.

During experiment 1 trial 2 there were a total of 4 unique radio tags detected. The first clear identification of a white sturgeon on video occurs 2 minutes and 20 seconds after the start of the trial, while the ovarian fluid flow rate was at 100ml/min. One radio tag (code 18) was detected for 3 consecutive minutes indicating this fish was interested in locating the ovarian fluid source, although radio signal power remained low (maximum 64) perhaps indicating the fish did not accurately pinpoint the release location. A white sturgeon was identified in the video footage 50 seconds after code 18 was first detected. There is not enough information to identify the fish in the video footage as the fish tagged with radio code 18. However, the timing of code 18 detections and the positive identification of a white sturgeon on video suggest white sturgeon code 18 was able to pinpoint the release location despite the low power signal.

All of the white sturgeon identified on camera spent a very brief amount of time within frame. This may suggest the fish became disinterested with the ovarian fluid alone. Perhaps there are multiple cues that are necessary to elicit a spawning behavior pattern in white sturgeon. White sturgeon activity continues throughout the entire duration of trial 2. One sturgeon was clearly identified on camera approximately 10 minutes after trial 2 initiated and a radio tagged fish was detected for one minute approximately 15 minutes after trial 2 initiated.

Video footage clearly shows Northern pikeminnow are attracted to the odour source and displaying feeding behavior towards the ovarian fluid source. It is plausible to speculate that Northern pikeminnow could have evolved to recognize chemical cues from

ovarian fluid as prey cues that they can use to track down the region where white sturgeon eggs are laid. Other possibility could be that Northern pikeminnow are attracted to amino acids or protein components that are common in ovarian fluid (Rime et al., 2004). When combined with high density of Northern pikeminnow in the study area, evidenced by frequent appearance in the video, it warrants further investigations on the potential roles of Northern pikeminnow in predation on eggs and larval sturgeon, given that Nechako River white sturgeon population is currently experiencing recruitment failure, but that the specific contributing factors are still unclear.

From annual egg collection projects it is clear white sturgeon are engaging in the act of spawning, however those fertilized eggs do not appear to survive to juvenile ages. One possible explanation is a high predation rate from other species, such as Northern pikeminnow or bull trout. Video results from this project suggest Northern pikeminnow are especially adept at locating white sturgeon ovarian fluid release locations, and actively feed on it. It would be reasonable to assume Northern pikeminnow would also feed on fertilized and unfertilized eggs, as well as white sturgeon larvae.

No appearance of white sturgeon in video footage during our Experiment 2 was surprising because Experiment 2's release location was in an area where white sturgeon are typically detected via radio tracking, and a known spawning location. Therefore, radio detections during this experiment should be interpreted cautiously. Five radio detections occurred nearly within the same second, and one of those radio codes appears to be erroneous because there is no database record for that radio tag. Although the detection pattern appears odd, the other 4 tags detected at 17:29:13/14 are plausible detection codes. The burst of radio detections in Experiment 2 suggests a large initial dose (e.g. 100 ml/min for 5 min) attracted a group of white sturgeon near the release location, but only briefly. Interestingly, 3 of the 6 fish detected in Experiment 2 trial 1 were mature fish ready to spawn in 2015 (confirmed by visually inspecting gonad development during tagging events in 2015). Those radio-detected fish also had low power signals, which suggests the tagged fish did not swim close enough to be captured on video.

The total lack of sturgeon detections (both video and radio) during Experiment 2 trial 2 was an unexpected result. While the lack of video detections may not be surprising, the lack of radio detections after a large initial dose suggests any sturgeon that did sense the ovarian fluid was not able to track it back to the release location, perhaps due to an absent "scent trail". Another possible explanation for the lack of on-camera identifications is the video

camera may not have been pointing downstream thus making it nearly impossible to capture approaching fish.

The doses of potential chemical cues used in the present study were not unusual given the dilution factors of 2.25×10 , 400×10 , and 200×10 . If ovarian fluid contains any potential cues at a concentration of 10^{-3}M , the final pheromone concentrations downstream could range between 10^{-11}M and 10^{-13}M , which is not unusual given that fish are known to have highly sensitive olfaction: for example, sea lamprey can smell sex pheromone as low as 10^{-13}M (Johnson et al., 2009). However, there are two other factors to consider: 1) we do not know actual concentrations of potential pheromones in ovarian fluid; 2) White sturgeon's olfactory sensitivities are largely unknown. Therefore, it is premature the doses used were within the white sturgeon's olfactory capacity. Since it is well known that olfactory sensitivities are species specific, more conservative approaches may need to be considered in the future experiment.

Although the present study may suggest a possibility that ovarian fluid contain chemical stimuli, attracting mature males to the odour source, further studies are required to confirm the presence of attractive behavior mediated by the pheromonal compounds originating from ovarian fluid. First, not knowing the potency of the potential pheromonal compounds in ovarian fluid, it was virtually impossible to develop an appropriate dosing protocol for the experiment. Apparently, the doses used in the present study were not optimal in keeping male sturgeon occupied during the experiment. By considering the dilution factor in the river, the final concentrations of the potential pheromones needs to be adjusted and white sturgeon's responses to the varying concentrations can be examined. In addition, it will be advisable to devise a mode of application in order to sustain pheromone concentrations in the river and create concentration gradient that white sturgeon can use to zoom in to the odour source.

One limitation in the present study was that white sturgeon's movements were not traceable with a high resolution, making it difficult to determine whether fish were truly attracted to the odour source or not. By setting up radio receivers near the release site, the behavioral resolution can be improved.

In conclusion, this pilot study provided positive results for ovarian fluid acting as an attractant to adult sturgeon in a river environment. Experiment 1 resulted in a greater number of white sturgeon identifications on camera, perhaps because the release location was chosen based on confirmed presence of multiple white sturgeon downstream. In

addition the camera was clearly pointed downstream in Experiment 1. The high density of Northern pikeminnow at the ovarian fluid release location should be investigated further. Future experiments should test whether Northern pikeminnow are actively locating the release location of ovarian fluid, if they're simply at such a high density that they are captured on video by chance. Releasing a control fluid (river water) in addition to ovarian fluid and comparing the number of Northern pikeminnow captured on video should be a sufficient test. Experiment 2 also demonstrated adult white sturgeon near the area ovarian fluid was released, however no fish were captured on camera suggesting the fish were not interested, or unable to locate the ovarian fluid release location. The lack of video identifications may simply reflect a poorly set-up camera, thus future experiments need to ensure the mooring is deployed in such a way that ovarian fluid release nozzle and video camera are facing downstream. Future experiments should also manipulate the flow rates of ovarian fluid. The complete lack of detections in experiment 2 trial 2 suggest white sturgeon require a minimal "scent trail" to actually locate an area where ovarian fluid has been released. In addition to flow rate manipulations it may be interesting to provide additional spawning cues in an attempt to keep white sturgeon in the release location after they have found it.

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Fisheries and Oceans Canada
Canadian Science Advisory Secretariat (CSAS)
Regional Peer Review Process - Pacific

Written Review

Date: March 24, 2016

Reviewer: Steven McAdam, BC MOE

CSAS Working Paper: 2013/14 PXX [Chair to fill in Working Paper # and Title]

Working Paper Title: Recovery Potential Assessment for White Sturgeon (*Acipenser transmontanus*) Upper Fraser Designatable Unit

1. Is the purpose of the working paper clearly stated and aligned to the Terms of Reference for this CSAS Review?

All elements are addressed within the document. However, concordance between the working paper and the TOR would benefit from more explicitly identifying the 22 elements within the document. I have provided detailed comments indicated by page (P) and paragraph (p) for some of these elements.

With specific regard to allowable harm (element 22) the analysis suggests that the middle and upper Fraser groups are stable if current conditions are maintained and no exchange is assumed. Allowable harm under scenarios that include exchange are affected by uncertainty regarding actual exchange rates and future stocking. As a result, allowable harm until those scenarios still has substantial uncertainty.

2. Are the data and methods adequate to support the conclusions?

I have some concerns that are noted below. In particular assumptions regarding exchange rates and Nechako stocking rates have a very dominant effect on results. There is substantial uncertainty regarding suitable exchange rates. The high scenario of 5% certainly appears too high based on current results. Similarly results clearly suggest that the assumed stocking rate would lead to unintended consequences. I would expect stocking rates to decline if the predicted results were observed. Therefore the assumption of a stable (and high) stocking rate over the modelling period appears unrealistic. Given the uncertainty in these two key assumptions further scenarios would need to be considered in order to make results most useful for supporting management decisions.

3. Are the data and methods explained in sufficient detail to properly evaluate the conclusions?

The data and methods are explained, although I found a few locations where the description of results was unclear (see detailed comments). Also, given the dominant effect of hatchery inputs and my expectation that these will change (i.e. decline), the absence of other scenarios makes evaluation of some conclusions somewhat moot (i.e. scenarios affected by hatchery inputs).

4. Is the working paper aligned to the objectives in Terms of Reference?

In a general sense yes, but I did find a number of locations where the material did not appear to be as up to date as it could be. I have detailed these concerns in my comments below. Most specifically this regards the presentation of the causes of recruitment failure, for which the inclusion of other information could have focussed attention on changes to spawning and early rearing habitat, and the current habitat restoration efforts.

5. Does the advice reflect the uncertainty in the data, analysis or process?

Sources of uncertainty are indicated in the report. Consideration of the two life history settings does address the effects of uncertainty in most parameter settings. However, future changes in stocking rate are not addressed, but should be. Additional means to evaluate reasonable levels of exchange would also be valuable. For example, demographic differences between the Nechako (long term recruitment failure) and the middle/upper Fraser indicate that exchange into the Nechako of juveniles must be very low or absent. Genetic differences might also provide some indication of the level of exchange, although reproductive exchange can be achieved without demographic exchange.

6. Are there additional areas of research that are needed to improve the quality of or the ability to provide advice and recommendations related to the stated objectives?

Additional areas of research largely flow from the comments above. Evaluation of different stocking rates and methods to evaluate exchange rates are two areas that would be particularly beneficial.

General comments

- 1) The report indicates that upper and middle Fraser populations will meet abundance targets if current conditions are maintained, and even with small changes to Habt and HM. This finding is largely a result of model assumptions. To strengthen this assertion some evaluation of possible current trends would be valuable, though I appreciate the data limitations in doing so.
- 2) The Nechako population is undergoing recruitment failure and responses for that population are dominated by the effects of supplementation. This dominant effect of one assumption (stocking at 12,000/year) is addressed further below.
- 3) Exchange rates – These also have a strong effect on results, so it is imperative that further consideration is given to whether they are reasonable assumptions. This is also addressed below. What level of exchange is compatible with current population differences? Genetic differences may be challenging to evaluate, but demographic differences may be more amenable to analysis. For example, the demographic differences suggest that there is near zero exchange into the Nechako.

Stocking rates

The report shows that results for the Nechako are dominated by hatchery inputs. This dominant effect of hatchery inputs affects the Upper Fraser groups at 0.1% and 5% exchange, and the Middle Fraser group at 5% exchange. The strong effect of stocking in the Nechako creates some challenges. In particular I expect that stocking rates will likely decrease over time. I expect this decrease will occur for two reasons. First, if the results predicted in this analysis are observed then I expect stocking rates would be reduced. Monitoring is currently in place to evaluate movements of white sturgeon out of the Nechako, so even considering the model assumption that exchange is limited to adults (this assumption is addressed below) I would expect that the maximum period for high stocking rates would be ~25 years. However, monitoring regarding juvenile abundance and survival would support changes much earlier than that, and I would predict changes could occur within 5 years. Secondly, habitat restoration efforts in the Nechako are being pursued, and at some point should supplant hatchery stocking. While we can't set a date for this, I expect this will occur within 10 years and definitely within 50 years. So my overall concern is that the assumed continuation of stocking for 100 years leads to modelled results that are unrealistic. This assumption primarily affects the Nechako group, with effects on the other two groups depending on the assumed exchange rates.

Exchange rates

Three exchange rates were considered (0, 0.1% and 5%). My understanding is that the 5% exchange rate was intended to provide a high assumption. While I believe it achieved that goal, the results appear unreasonable and therefore may be uninformative. The two lower scenarios appear more informative, however, even the low level exchange leads to substantial effects under current stocking assumptions. Further evaluation of exchange assumptions against other indicators would be beneficial. For example, can we estimate exchange rates from movement data, genetic data or demographic data? As noted above demographic differences suggest no exchange into the Nechako River for fish under 40-50 years old. One could evaluate the maximum exchange rate that could occur while still observing the present demographic differences. Also I believe the model assumes the same level of exchange between two groups, but the basis for this is unclear.

Additionally the logic of demographic exchange is somewhat unclear. The model assumes that exchange occurs for adults. While very low exchange rates would be hard to detect for any population how well does this assumption match observations for other sturgeon? The genetic differences identified in other studies (Smith et al., Schreier et al.) appear to influence the assumed pattern of exchange (i.e. no direct exchange from Nechako to Middle Fraser), however, reproductive exchange and demographic exchange are distinct. So the logic of this assumed exchange pattern is unclear.

Specific comments (P=page, p=paragraph)

P2p2 You might mention their presence in tributaries. Presence has been confirmed for the Seton (fish found on Seton trash rack) and the Thompson (capture in Kamloops Lake). Available evidence suggests

use of these areas may be occasional (except the Seton fish was trapped upstream by the dam – this statement is based on my analysis of the fish’s fin ray chemistry).

P4 – 2.3.4 “At the onset of the feeding larval period...”

P5 p1 The Semakula and Larkin (1968) reference is for the lower Fraser. While they may provide a general indication for the species this range may be less relevant to the Upper Fraser DU.

P5p5 The reference to spawning in side channels is for the lower Fraser. Seems unlikely to be as relevant in this DU due to a) the more limited abundance of side channels (e.g. middle Fraser is largely canyonized), b) lower volumes so side channels smaller c) loss of side channels in the Nechako (see ref in McAdam et al. 2005) and d) confirmed mainstem spawning in the Nechako.

P5p6 I don’t think the prevalence of repeat spawning is the best wording. I’d say there is certainty that it occurs, but uncertainty about the interspawning interval.

P5p7 White sturgeon are iteroparous (i.e. omit “may also”). Additionally, I would not use Semakula and Larkin in this manner. It refers to the lower Fraser. These sorts of intervals appear to be longer than estimates from other sources (e.g. actual repeat spawners in the Kootenay and Nechako). Also, the methods underlying the estimates by Semakula and Larkin are spawning checks. I’ve never seen any other reference to spawning checks in sturgeon, so I question the validity of their estimates.

P6p2 The last sentence makes statements about movement. Some substantiation should be provided. For example, in this DU what evidence is there of dams altering movement patterns? The only example I can think of is a fish trapped in Seton Reservoir, but a single example doesn’t seem to warrant this sort of general statement.

P8p2 The middle Fraser is also distinct as it is canyonized through much of its length. This is somewhat unique (some other canyon populations in the Snake River, but that river is highly regulated).

P12p2 Seton and Thompson River examples are mentioned above and could be mentioned in this paragraph.

P13p4 It would be good to indicate the basis of the last sentence indicating the molluscs are likely prevalent in the diet?

P13p5 Spawning has been initiated at lower temperatures. I believe the lowest was between 11 and 12C. This occurred subsequent to Sykes’s work and should be included in the spawning reports. Cory Williamson or Brian Toth should have a better idea here.

P14p2 The reference to the lack of use in Kamloops Lake is out of date.

P14p5. In general the material referring to recruitment failure causation appears somewhat dated. For example the reference to Korman and Walters (2001).

P15p4 Again, I’m concerned that the reference to Korman and Walters (2001) is dated, though the statement here is generally correct. Since that time the Nechako TWG has done a lot of work

considering different hypotheses. Largely this culminated in McAdam et al. (2005), however, it is important that this study did not consider all hypotheses in a structured manner. That sort of approach was used in McAdam (2015), and again substrate change appears to be the causal mechanism in the Columbia River. A similar analysis is not available for the Kootenay though Paragamian et al. (xxxx) and McDonald et al. (xxxx) (see refs in McAdam 2015) also indicate substrate change is the likely cause in the Kootenay. Therefore, multiple studies in multiple rivers indicate a substrate mediated effect. While this is certainly not proof it provides stronger evidence than is implied in the current text. The importance of this is the potential for spawning habitat remediation, which we are actively working on. If successful (and I do expect we will have some success soon) then assumptions regarding hatchery stocking rates will vary. Given the dominant effect of hatchery stocking rate and survival assumptions, anything that may affect those stocking rates over the short and medium term deserves particular attention.

P15 4.1.1 I think the report should specifically mention changes to spawning habitat. There is good evidence that early survival is critical to recruitment, that spawning habitat is a particularly vulnerable habitat type, and that changes to spawning habitat have occurred.

P16p2. The lack of proof regarding causes of recruitment failure is important to acknowledge. However, there is increasing evidence of a substrate mediated cause (noted above). Given this I think uncertainty is over emphasized in this document.

P17p3. While the magnitude of illegal harvest is not known I believe there is evidence that it is not zero. This doesn't appear to have been captured in the current analysis (though might have little effect on the current analysis).

P18 p3 The use of habitat enrichment during early rearing may also yield some benefit with regard to adverse hatchery effects.

P20p3 Smelters doesn't seem appropriate for this DU.

P21p2 There are some terminology edits needed. Line 3 should be white vs. juvenile (sturgeon). Line 5 should refer to larval vs juvenile survival. The second half of this paragraph deserves some attention as there has been a substantial amount of work regard this particular impact. Lab studies are in McAdam (2011). These were extended to small scale field studies in McAdam (2012). This in turn led to larger scale field scale restoration experiments consisting of creating two spawning 'pads' in 2011. There are a number other reports on the fluvial geomorphology of the reach that might be of interest that further build upon this impact mechanism (see NWSRI website).

P24p1 What is the assumed generation time? I often use 40 years. If so 100 years doesn't capture 3 generations.

P24p4 The timing of recruitment failure appears incorrect. Best estimate is 1967, which is 49 years ago. That said the number of adults wouldn't have declined by 1976 so effects on adult abundance may be nil or minimal.

P25p4 From a modelling perspective I understand why you might only allow adults to move, but I'm not sure it is biologically realistic. There appears to be a discord between what we understand of their

behaviour and the model assumptions. Adult behavioural studies often indicate specific and repeated use of particular habitats. Some studies (Nelson and McAdam 2012) show highly resident groups. Other studies (Beardsall and McAdam 2016) show a split between resident and non-resident movement types in the lower Fraser. Assuming the latter there is a possibility of genetic exchange without demographic exchange. However, this model assumes both co-occur. There may be a need for some analysis to see how likely this is given our current understanding of demographic and genetic differences between these groups. This may inform the likelihood of each of the exchange scenarios.

P42p2+3 – There appear to be inconsistencies in the text with regard to the 0% exchange scenario. Paragraph 2 indicates that the 0% scenario doesn't achieve 100% of target abundance. Paragraph 3 indicates that the 0% exchange achieves the target abundance. I assume the paragraph 3 version is correct. The paragraph 2 statement may refer to the 0.1% exchange, but the reader shouldn't need to figure this out.

P44p1+2 Same issue as above but for the upper Fraser group.

P50p3 typo 1999; pers comm is Cory Williamson

Nechako River White Sturgeon Spawn Acoustic Monitoring 2015 Results

Rev. 2
October 3, 2016
Prepared for

Nechako White Sturgeon Recovery Initiative Technical Working Group (NWSRI - TWG)

Prepared by Jeffrey Beardsall and Dr. Steve McAdam

32	Table of Contents	
33	List of Figures.....	3
34	List of Tables	Error! Bookmark not defined.
35	Introduction	4
36	Materials and Methods	5
37	Study System and Receiver Deployment	5
38	Spawn Monitoring using Egg Mats	8
39	Radio Telemetry Efforts.....	8
40	Acoustic Tag Deployment.....	8
41	Vemco Positioning System (VPS) and Acoustic Telemetry.....	9
42	Receiver Retrieval and Processing	Error! Bookmark not defined.
43	Results	11
44	Egg Mats	11
45	Hydrometric Data.....	14
46	Acoustic Telemetry – VPS Performance	15
47	Acoustic and Radio Telemetry - White Sturgeon Detections.....	16
48	Acoustic Telemetry - Spatial Distribution of White Sturgeons within VPS Array	18
49	Acoustic Telemetry - Sturgeon Trajectories.....	20
50	Discussion	25
51	References.....	28
52	Appendix A : Tables	29
53		
54		

List of Figures

Figure 1. Map of Nechako River spawning system including marked locations for radio receivers (blue filled triangle), acoustic receivers (red filled circle), egg mat sites (yellow “x” square), and VPS array detection zone containing 18 acoustic receivers (red open rectangle). Inset map shows location of spawning reach (red open rectangle) in context of central British Columbia.	7
Figure 2. Small-scale map of Nechako River spawning reach. Black circles represent acoustic receiver locations participating in the VPS array. The diameter of the black circles approximates detection range. The area shaded light gray is the location of the lower patch. Note water level was relatively high in 2015, and the map riverbanks in this figure reflect high water conditions.	10
Figure 3. Egg mats hit with eggs between May 11 and May 19 th in top panel, egg mats hit with eggs between May 19 and May 21 in middle panel, and egg mats with eggs between May 21 and May 23 in bottom panel	13
Figure 4. Mean daily discharge rates measured at Burrard Bridge, Vanderhoof, BC. Data within the green rectangle were recorded during the 2015 white sturgeon spawning period (May 19 to May 23).	14
Figure 5. Mean daily water temperatures recorded by sensors located at Burrard Bridge (filled circles) and attached to acoustic receiver in VPS array (lines). The two sensor records almost always match each other. Data within the green rectangle were recorded during the 2015 white sturgeon spawning period (May 19 to May 23).....	15
Figure 6. Linear relationship between horizontal positing error (HPE) values and mean positioning error estimates. Error bars show 1.0 standard deviation. Note at horizontal position error 11 the upper range of mean positioning error jumps to ~15m.....	16
Figure 7. Number of sturgeon positions and number of unique sturgeon in VPS array by date. Greatest number of sturgeon positions occurs on May 19 th , 2015 followed by May 20 th . Those are also the two days with the greatest number of unique sturgeon (5) positioned in the VPS array.....	17
Figure 8. Each panel shows the entire relocation dataset for each acoustically tagged white sturgeon (acoustic tag ID in grey panel-header). The gravel deposit is outlined in white.	19
Figure 9. Nechako River white sturgeon (acoustic ID 24748, Male) trajectory bursts divided into days during the spawning period.	21
Figure 10. Nechako River white sturgeon (acoustic ID 24750, Female) trajectory bursts divided between days during a spawning event in 2015.....	22
Figure 11. Nechako River white sturgeon (acoustic ID 24752, Female) trajectory bursts divided between days during a spawning event in 2015.....	23
Figure 12. Nechako River white sturgeon (acoustic ID 24754, Male) trajectory bursts divided between days during a spawning event in 2015.	24
Figure 13. Nechako River white sturgeon (acoustic ID 24756, Male) trajectory bursts divided between days during a spawning event in 2015.	25

Introduction

As of July 2016 the Nechako River white sturgeon population status is Critically Imperiled (S1) as assessed by British Columbia Conservation Data Center (BC CDC). This species was also legally designated as Endangered under SARA in 2006. The ongoing population decline resulting from chronic recruitment failure was the primary reason for the endangered designation. Current understanding suggests ongoing recruitment failure, but the exact mechanisms behind the failure aren't clearly understood

Restoration of successful natural recruitment in the Nechako River white sturgeon population is the principle goal of the recovery program directed at this population.

Although white sturgeon occupy many habitats throughout the Nechako River watershed (e.g. Nechako River, Stewart River, Stewart Lake, Fraser Lake) the only spawning sites identified to date are located within a roughly 2 km river reach near Vanderhoof BC.

Recruitment failure is the apparent result of historical habitat degradation that increased sand deposition throughout the spawning reach (McAdam et al. 2005). Additionally, hydraulic modeling and spawn monitoring studies suggest that white sturgeon spawning locations may have shifted as compared to the historical (pre-regulation) conditions (NHC 2003; 2012; Triton, 2010). The planning of future habitat restoration must therefore ensure that restoration occurs in areas that are actively selected by spawning white sturgeon. The use of 2 dimensional acoustic positioning (Vemco Position System, or VPS) array was selected to examine fine scale spawning habitat selection, and also to evaluate the extent to which spawning activities occurred within the areas where spawning substrate was experimentally restored in 2011 (NHC 2012). Two particular areas where restoration occurred are referred to as the middle and lower patch.

The current hypothesis suggests infilling of the interstitial spaces in river substrate could result in poor larval survival and therefore poor recruitment of juveniles into the population. River substrates in the spawning reach progress from coarse cobble in the upstream areas to fine sediments in the downstream areas. While a minor improvement in juvenile recruitment was detected after substrate remediation efforts in 2011, responses were likely affected by substrate infilling shortly after these habitats were created, and prior to the 2011 spawning season.. The downstream spawning habitats (e.g. lower patch site) are experiencing the greatest amount of infilling (NHC 2013).

Radio telemetry and egg detections from previous spawn monitoring years suggest white sturgeon select spawning sites within the spawning reach depending on flow conditions (unpublished data). During high flow years it appears white sturgeon tend deposit eggs in the downstream areas of the spawning reach (e.g. lower pad site and downstream of Burrard Bridge). During low flow years it appears white sturgeon tend to deposit eggs in the upstream areas of the spawning reach, including a high water-velocity area with cobble-dominant substrate (Triton 2010) and the braided channel/island complex area including the main southern channel and upper pad remediated site. It is important to target monitoring efforts appropriately considering the flow conditions for the year. Spawn monitoring in the Nechako River spawning reach has been a multipronged approach. The initiation of spawning events are fairly predictable thanks to data collected in previous years from egg detection mats, radio telemetry, adult sampling, and underwater video efforts. While the timing and general area of spawning is known, fine-scale spawn site locations are unknown. It is also unclear whether or not white sturgeon occupy remediated areas within the spawning reach. The inclusion of the VPS in 2015 spawn monitoring efforts was intended to investigate fine-scale location occupancy within the spawning reach during the spawning period.

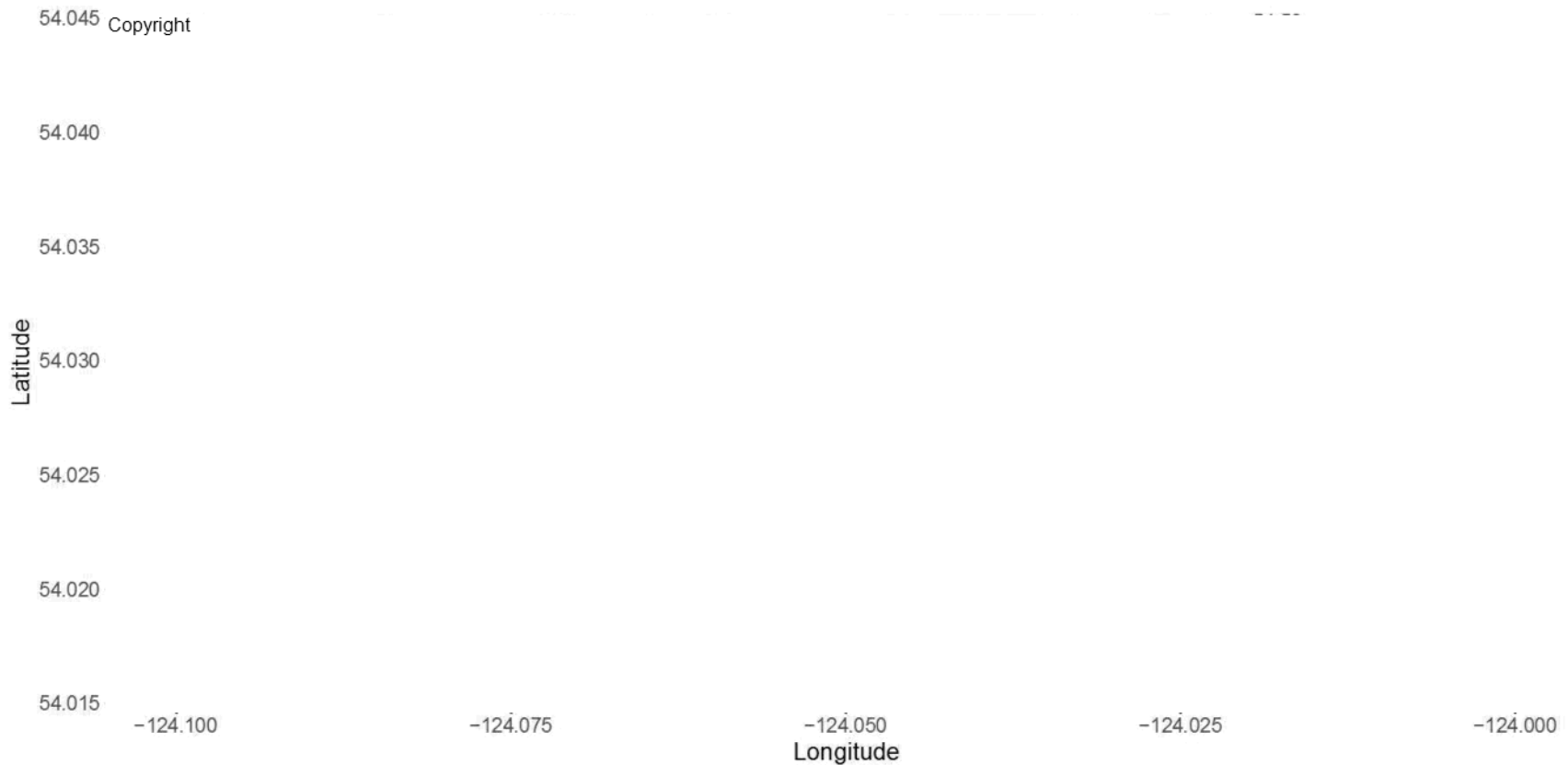
Materials and Methods

Study System and Receiver Deployment

The Nechako River white sturgeon spawning reach (Figures 1 and 2) includes several important locations and hydraulic conditions. These local conditions vary with flow magnitude. Understanding some of these key locations provides important context in the present study and they are considered here from upstream to downstream. The single thread channel of the Nechako River immediately upstream of the spawning reach is an area that shows elevated velocity over a range of flow conditions. Although historical evidence is lacking the working assumption is that area represented the historical spawning location for this population. Within the central area of the spawning reach the river channel is braided and flows around an island complex. At high velocity (e.g. historical spawning conditions, see NHC 2006) water velocities in this area decreased due to the backwatering effect as flow

160 was constricted by the landforms adjacent to the Burrard Avenue Bridge. However, at lower
161 flows that now occur over much of the year the main channel flows to the south of the main
162 island complex, and elevated water velocities occur at the outside bend of meanders. Two
163 such locations where elevated water velocity has been associated with spawning are just
164 downstream of the Stoney River confluence and immediately upstream of the Burrard
165 Avenue Bridge. Both of these locations were selected for experimental spawning habitat
166 restoration (see NHC 2013), and are referred to as the upper and lower pads, respectively.
167 Immediately downstream of the lower pad is the Burrard Avenue Bridge which forms a
168 unique hydraulic feature at this fixed location. The combined effects of flow constriction
169 due to the landforms on either side of the bridge and the mid channel bridge abutments
170 leads to high water velocities associated with the bridge location over a range of flow
171 conditions. While spawning has not been detected in the immediate vicinity of the bridge
172 eggs have been collected downstream of the bridge, and the area for ~500 m downstream of
173 the bridge is considered the fourth area where spawning has been repeatedly detected.

174



175

176 *Figure 1. Map of Nechako River spawning system including marked locations for radio receivers (blue filled*
177 *triangle), acoustic receivers (red filled circle), egg mat sites (yellow "x" square), and VPS array detection zone*
178 *containing 18 acoustic receivers (red open rectangle). Inset map shows location of spawning reach (red open*
179 *rectangle) in context of central British Columbia.*

180

Egg Mats

Egg collection procedures in 2015 were the same procedures used in previous years (Triton, 2010). Egg mats were constructed using 1m by 1m polyurethane industrial filter material sandwiched between two angle iron frames. Each frame had one or two wooden cross-members to provide stability for the filter material. Two egg mats were joined end to end using a carabineer and deployed together at particular sites. A bright orange buoy was also attached using ~ 8 m buoy line tied to the upstream end of the mats, which allowed for easy identification and retrieval.

Deployment depths were recoded using depth sonar sensor onboard the deployment boat. Water velocities were not recorded in lieu of discharge measurements recorded continuously at Burrard Bridge and downloaded from Government of Canada's Wateroffice website using station number 08JC001.

Radio Telemetry

Radio tags have been applied Nechako River white sturgeon over many years, and currently it is estimated that there are XXX active radio tags (check). An additional fifteen (15) radio tags (Lotek) were applied during 2015 brood capture program led by Freshwater Fisheries Society of British Columbia (FFSBC) employees Cory Williamson and Mike Mankey. This report only includes radio detections if they are directly related to VPS operations within the spawning reach. For that reason radio detections from stationary radio receivers only will be included. For a comprehensive report on radio telemetry detections in 2015 refer to the 2015 Nechako River Spawn Monitoring report (Carrier Sekani Tribal Council report in progress).

Brood Capture and Tag Deployment

The application of acoustic tags to white sturgeon was conducted in conjunction with broodstock collection activities and a predetermined formula was used to allocate captured fish either to the hatchery program or to tagged and releases as part of the VPS spawn monitoring study Adult white sturgeons were targeted using 20-80m setlines with 6-24 hooks per line; 16/0 circle hooks were used. Captured adults were processed and checked for sexual maturity. All adult fish were released with PIT and radio tags, and a subset were selected for acoustic tagging. Processing procedure for morphometric data was identical to

2009 procedures reported by Triton (2010). After all morphometric data had been collected a 1-2 cm incision was made on the ventral surface of the fish in between the 3rd and 4th scute from the anal fin. An otoscope was used to complete an internal exam of the gonads to assess sexual maturity. Spawning fish were either carefully taken back to transport tanks and brought to the hatchery as brood stock, or tagged and released immediately. Handling treatments differed between fish held for brood or fish tagged and released immediately, however the surgical procedure for tag implantation was identical for all fish released with tags. In order to accommodate the radio and/or acoustic tag the internal assessment incision was opened to approximately 4 or 5 cm. A V16-5xp VEMCO acoustic transmitter (60-80 second delay) was inserted anteriorly through the incision. Then a narrow gauge needle was inserted 2-3cm posterior to the incision, and pulled anteriorly through the incision. The radio tag antenna was fed through the hollow needle and the needle was removed leaving the antenna to trail external to the fish. Then a radio tag (Lotek) was inserted through the incision and slid anteriorly. Two or three sutures were tied to close the incision.

Vemco Positioning System (VPS) and Acoustic Telemetry

VPS test array deployments occurred during summer 2013, and during spring 2015. 2013 deployments found that the bridge abutments interfered with acoustic signal transmission and posed a problem for deploying one operational array upstream and downstream of the bridge. The test array in spring 2015 was meant to test acoustic transmission in 2015 environmental conditions (high water flow). Results indicated 80% detection efficiency at 60m spacing for most locations in the array. The exceptions were locations near Burrard Bridge abutments. Given acoustic performance and acoustic receiver resources the operational array was spaced 50m in the North-South direction of the array, and 60m in the east-west direction (Figure 2). The operational array was only deployed upstream of the bridge to focus monitoring efforts on the lower patch remediated area.

Eighteen VR2W acoustic receivers (VEMCO Ltd, Halifax Nova Scotia) were deployed in Nechako River in the proximity of the lower gravel pad to form a VPS array. VPS coverage included nearly all the area of the lower pad as well adjacent and upstream areas (Figure 2). Receivers were mounted on custom anchors constructed from two railroad tie plates

welded together, one 1.5m length of 3/8" construction rebar welded to the center point of the plates, and four 0.4 m lengths of 3/8" rebar welded to the plate corners to stabilize the anchor. VR2W receivers were attached to the rebar using a combination of industrial strength zip-ties, electrical tape, and duct tape.

VR2W receivers were retrieved on July 30, 2015. CSTC personnel downloaded receivers and data were compiled in one library. That library was sent to VEMCO for data processing. VEMCO returned a package containing raw transmitter position files in .csv format, Google Earth .kmz animation files grouped by transmitter ID and date of detections, and various supplemental files. Analyses presented in this report were run on the raw transmitter position files.

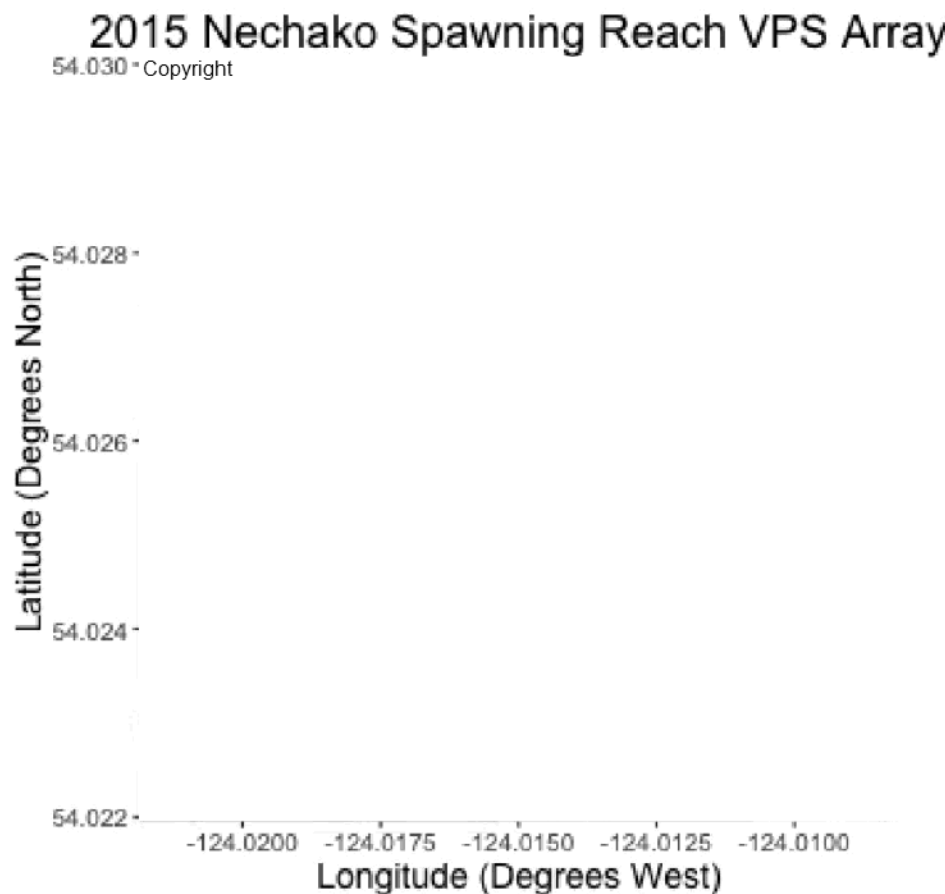


Figure 2. Small-scale map of Nechako River spawning reach. Black circles represent acoustic receiver locations participating in the VPS array. The diameter of the black circles approximates detection range. The area shaded light gray is the location of the lower patch. Note water level was relatively high in 2015, and the map riverbanks in this figure reflect high water conditions.

Results and Discussion

Brood Capture and Tag Deployments

Thirty-six adult white sturgeon were captured between April 14 and May 23, 2015. Nineteen fish were males, of which six (6) were flowing males (code 5). Five of the flowing males were held for brood stock, and one was released immediately with acoustic and radio tags. The remaining 17 fish were female, and ten (10) were ripe females (code 15). Six of the ripe females were held for brood stock, and four were released immediately with acoustic and radio tags. A total of seventeen acoustic tags were deployed; nine in immature fish (6 males and 3 females) expected to spawn within the life expectancy of the tags but not in 2015, five in mature fish (1 male and 4 females) released before or during the 2015 spawning period, and three in mature fish (all three male) held for 2015 brood stock. Twenty-two sturgeon were released the same day they were captured. Of those 22 released immediately, six were released with new radio tags, and eleven were released with acoustic tags. Of those eleven released with acoustic tags, five were immature fish not expected to spawn in 2015. Two of the 11 were likely 2015 male spawners, and the remaining three were 2015 female spawners. Fourteen adults were held as brood stock at the Nechako White Sturgeon hatchery. An additional seven acoustic tags were applied to brood fish after spawning and released back into Nechako River by June 02, 2015. Table 1 (Appendix A) displays all of the fish captured and released or held for brood stock. Flowing males (code 5) and ripe females (code 15) are highlighted in yellow.

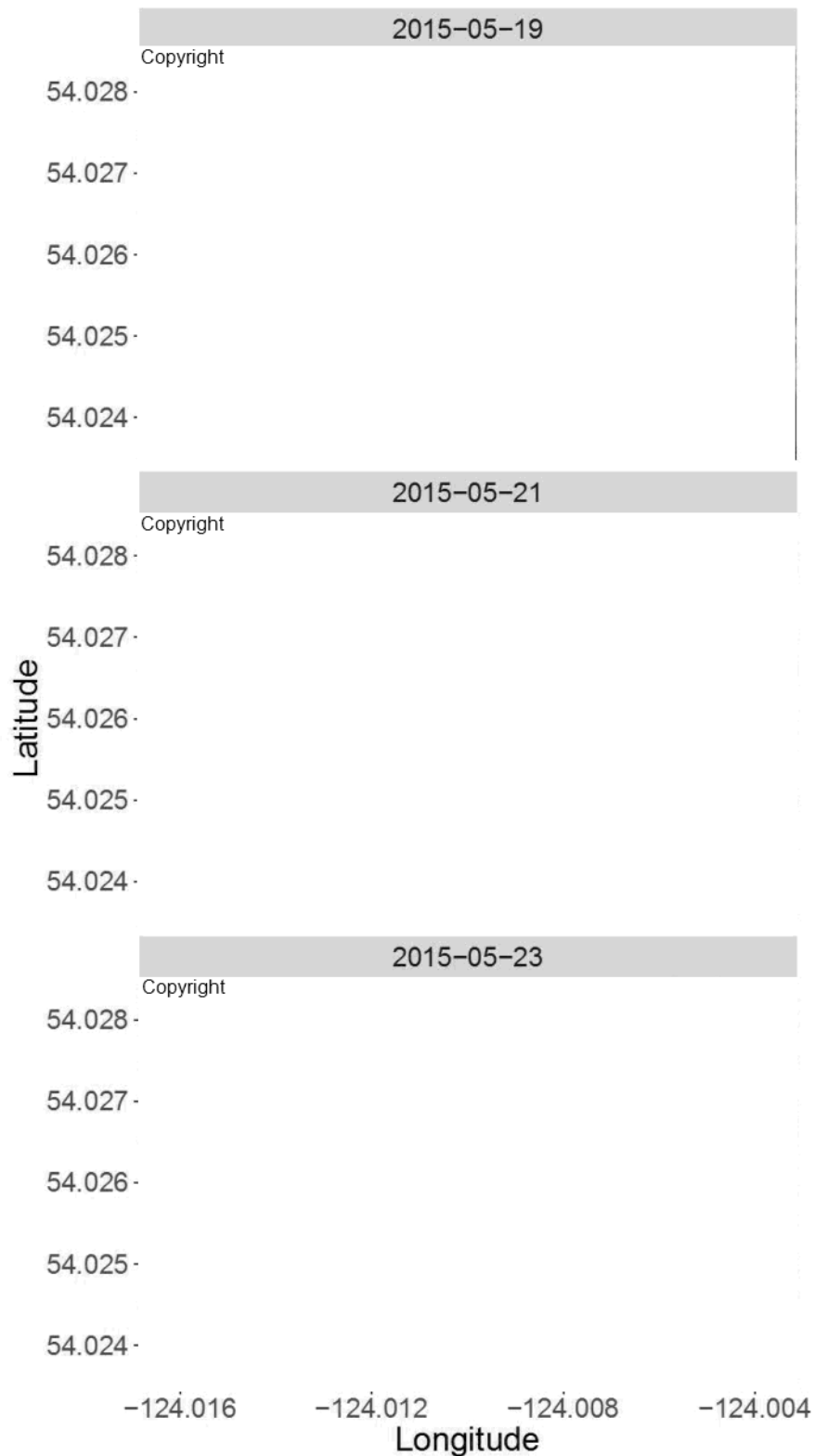
Egg Mats

Forty-six mats (twenty three different sites) were deployed on May 11, 2015. An additional 20 mats were deployed at 10 sites below Burrard Bridge on May 19th, making a total 66 mats deployed (33 sites) on May 19, 2015. All 33 sites were checked on May 21st and May 23rd. All 66 mats were pulled from the river on June 1, 2015 after having 0 egg hits since May 24th.

Three hundred and forty-two (342) white sturgeon eggs were recovered from Nechako River spawning reach. The dates of these collections indicate when spawning definitely occurred, as compared to the failure to detect eggs which provides a non- definitive indicator that spawning did not occur.

287 Eggs were collected on May 19 (25), May 21 (289), and May 23 (28). On May 24 only mats
288 located within the acoustic array were checked and no eggs were recovered. All of the mats
289 were checked and pulled on June 1, 2015. All of the eggs were detected below Burrard
290 Bridge, among the 15 egg mat sites that cross the channel in three rows of five..
291 Having all egg detections below Burrard Bridge is an interesting result because of flow
292 patterns at those sites. Generally it is assumed spawning activities occur very close to
293 positive egg detections, but perhaps the sites with positive detections in 2015 were the
294 result of drifting eggs being funneled into the narrowing channel in the bridge area.
295 Egg detections downstream of Burrard Bridge are significant because the VPS only covered
296 area above the bridge. Expanding the coverage of VPS both upstream and downstream will
297 provide insight on habitat use outside of remediated areas.

298



299

300 *Figure 3. Egg mats hit with eggs between May 11 and May 19th in top panel, egg*
 301 *mats hit with eggs between May 19 and May 21 in middle panel, and egg mats with*
 302 *eggs between May 21 and May 23 in bottom panel*

Hydrometric Data

River discharge was relatively high in 2015. On May 1, 2015 discharge measured approximately 500 m³/s (1 m³/s = 1 cubic meter per second), compared to approximately 200 cms in 2009 (Triton 2010). Spawning events (May 19 to May 23, 2015) occurred at discharge rates between 550 and 595 cms (Figure 4; green box covers spawning period). Note spawning occurred during an uptrend in discharge in 2015, but in 2009 spawning occurred during a downtrend in discharge.

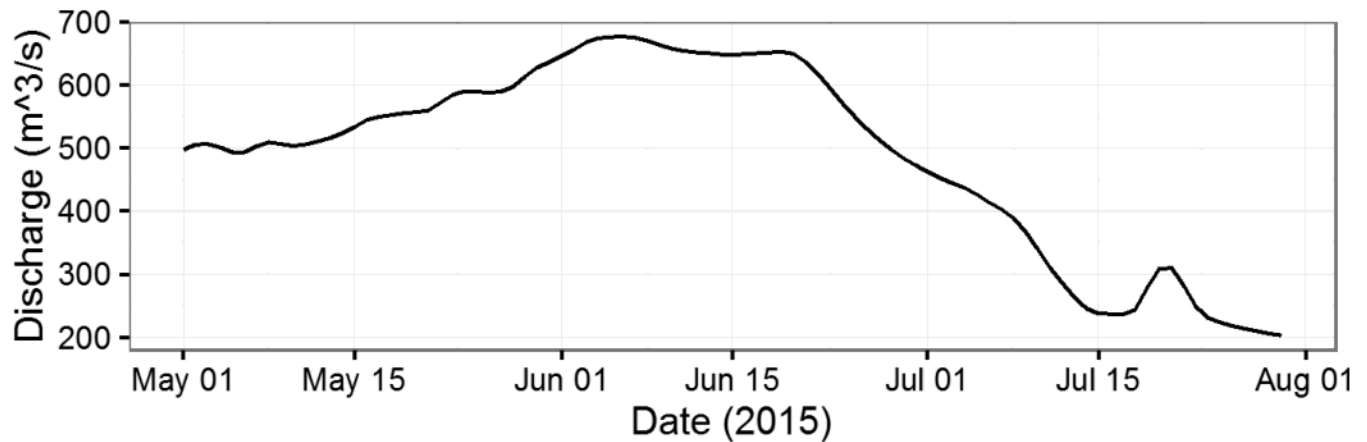


Figure 4. Mean daily discharge rates measured at Burrard Bridge, Vanderhoof, BC. Data within the green rectangle were recorded during the 2015 white sturgeon spawning period (May 19 to May 23).

Water temperature data were taken from two sources; the temperature sensor from Burrard Bridge, and a temperature logger deployed on acoustic station 3. Figure 5 shows mean daily bridge temperatures as filled circles, and the range of daily values recorded by the acoustic temperature logger as lines. Both sensors recorded temperatures between 10.5°C and 12.4°C during the spawning period (green box in Figure 5). The bridge sensor daily mean almost always matched temperatures in the lower range of the acoustic sensor. Two exceptions on May 6 and May 20, 2016 are clearly erroneous data points (May 20 bridge sensor data point not on scale, temperature = 32°C).

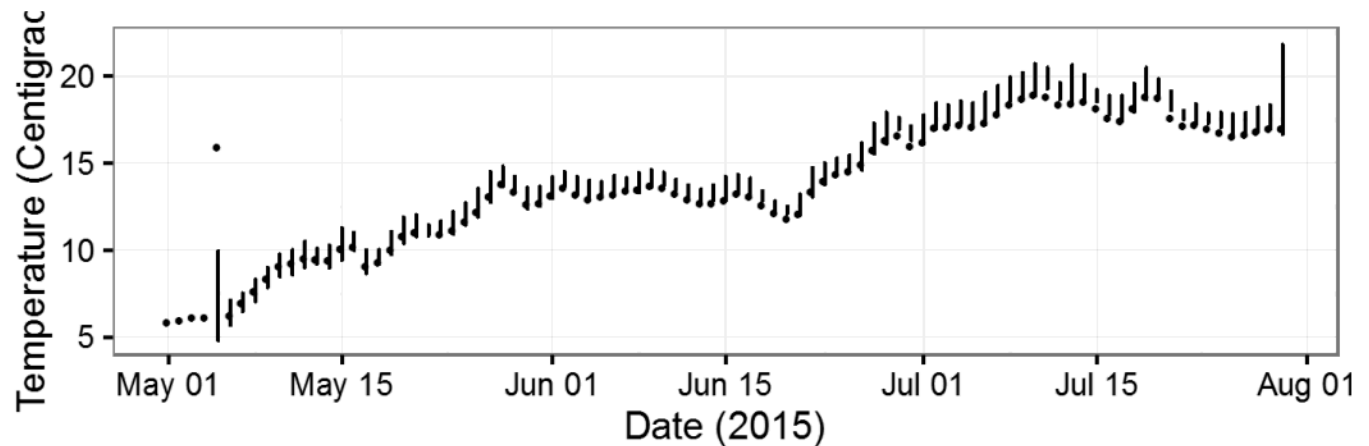


Figure 5. Mean daily water temperatures recorded by sensors located at Burrard Bridge (filled circles) and attached to acoustic receiver in VPS array (lines). The two sensor records almost always match each other. Data within the green rectangle were recorded during the 2015 white sturgeon spawning period (May 19 to May 23).

Acoustic Telemetry – VPS Performance

The VPS deployed in Nechako River spawning reach was functional May 05, 2015 13:30:00 PST until July 30, 2015 18:00:00 PST (86 days, 4 hours, and 30 minutes). Overall synchronization tag (sync tag) positioning percentages varied between 12.5% and 89.0%, and a mean positioning rate of 72.7% (Appendix A Table 2). These results indicate the VPS array was successfully positioning tags within the array approximately 73% of the time, depending on location of the tag within the array. The low positioning percentages of Stn16, 17, and 18 was expected due to acoustic interference from nearby bridge abutments Stn17 was moved by river debris rendering it inoperable for a large portion of the array deployment.

Studies using VPS normally filter their data based on a unitless value of error associated with the position calculated called the horizontal position error (HPE) prior to spatial analysis. To help inform researchers of an appropriate HPE filter criterion a spatial positioning error can be calculated for known tag locations, and then HPE values can be associated with a measure of position error. HPE values ranged from 7.6 to 169,282.4 in the unfiltered data set. Figure 2 shows the mean positioning error associated with HPE values grouped into bins of 1 and shows that a lower HPE filter leads to greater location accuracy. However, filtering using a lower HPE leads to fewer detections being included in the analysis. In an effort to balance acceptable position accuracy and minimize sample loss we

chose to filter our data to include HPE values less than 10.0. From our associated positioning error we can be confident most of our sturgeon positions are accurate within 10m, and mean positioning error is 3.3m.

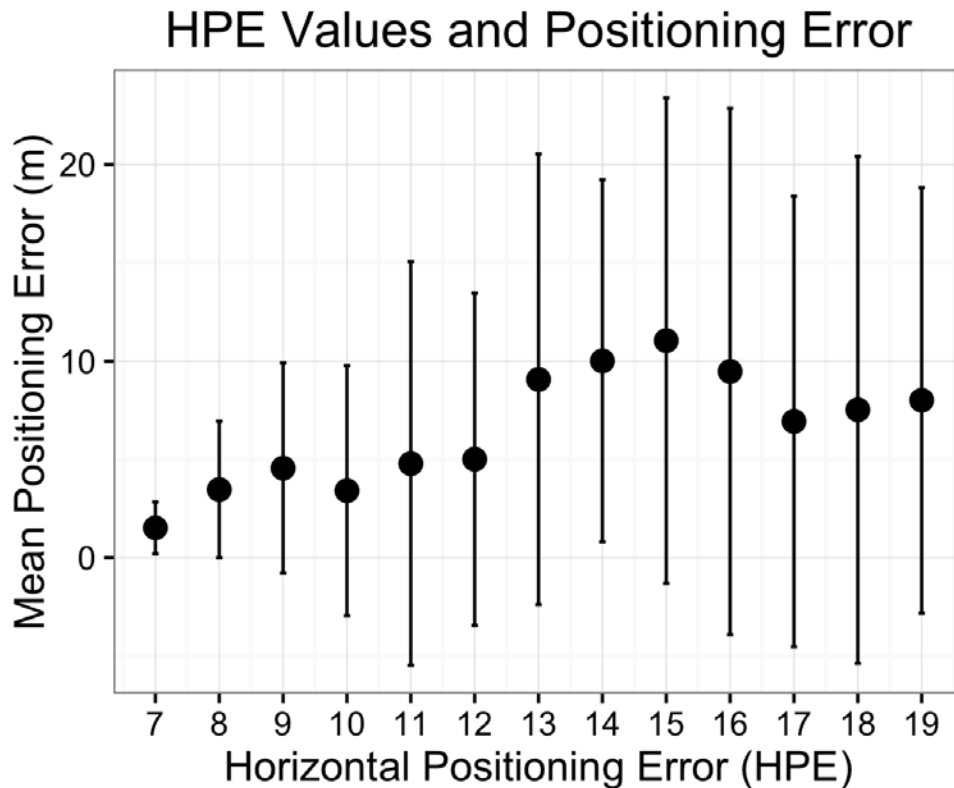


Figure 6. Linear relationship between horizontal positing error (HPE) values and mean positioning error estimates. Error bars show 1.0 standard deviation. Note at horizontal position error 11 the upper range of mean positioning error jumps to ~15m.

Acoustic and Radio Telemetry - White Sturgeon Detections

Evaluation of unfiltered data indicate white sturgeon detections on 44 out of the 88 of the operational days based on a total of 13,106 sturgeon positions from 9 sturgeons. The number of detections within the array varied over the spawning period with the greatest number of sturgeon positions detected on May 19th, followed by May 20th, 2015 (Figure 6). Those two days also have the greatest number of unique sturgeon (5) positioned within the array on that day.

Not all of the acoustically tagged sturgeon at large during the spawning period were detected in the VPS. Two ripe females were released on May 17 and May 19, respectively. Neither of those fish were detected within the spawning reach. This may reflect capture and

tagging stress, where those females opted to forgo spawning and either wait until 2016, or perhaps reabsorb their eggs and begin a new reproductive cycle. Their absence may also indicate there are suitable spawning sites downstream of the VPS array and Burrard Bridge.

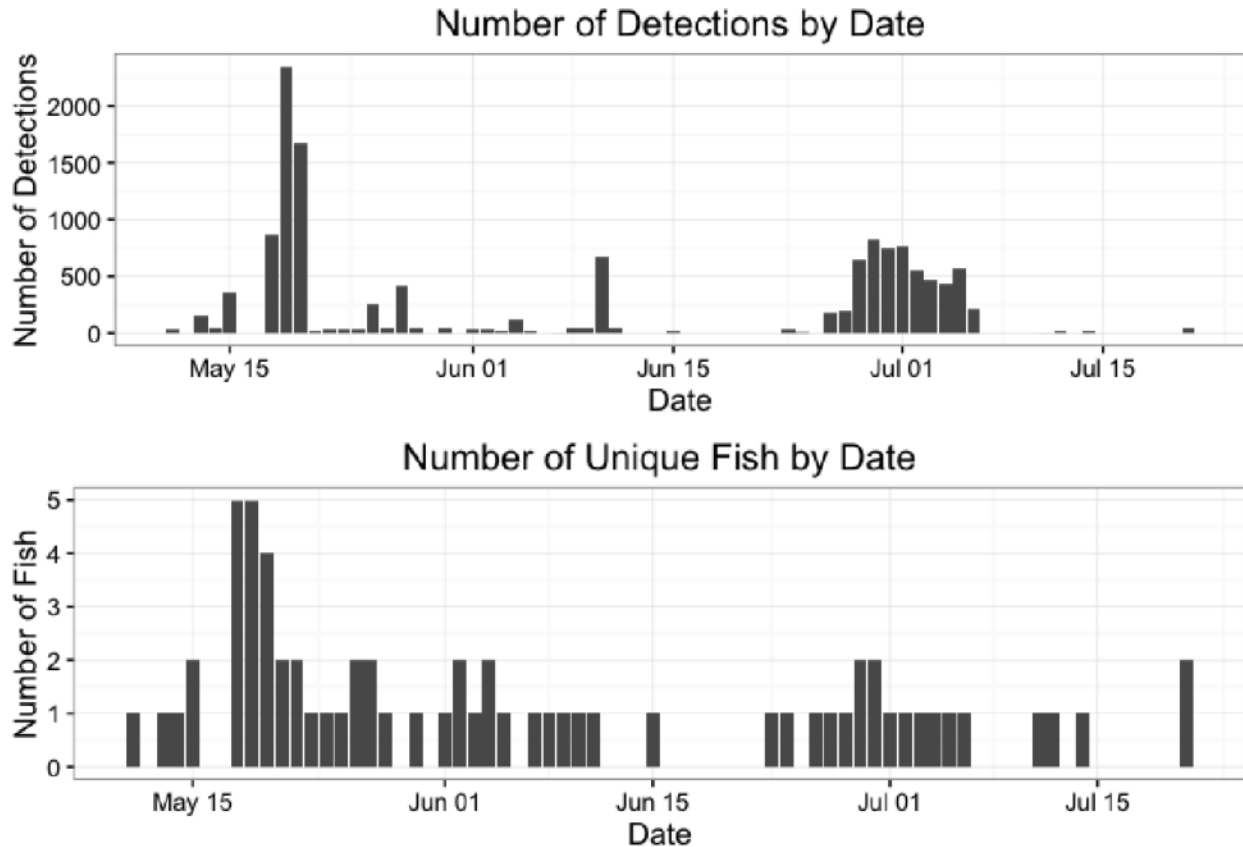


Figure 7. Number of sturgeon positions and number of unique sturgeon in VPS array by date. Greatest number of sturgeon positions occurs on May 19th, 2015 followed by May 20th. Those are also the two days with the greatest number of unique sturgeon (5) positioned in the VPS array.

Filtering our data using HPE < 10 criteria resulted in a sample of 7694 positions (58% of the unfiltered total) from 8 white sturgeons. Table 3 (Appendix A) summarizes the biological details and Table 4 summarizes detection activity of only the white sturgeon included in the filtered data sample.

Consideration of the data from acoustic and radio telemetry tags collective provides an understanding of the periods when white sturgeon were present in the spawning reach. Two mature females were included in the 2015 study. These were tagged and released in early May, and these females were first detected in the VPS array on the May 18, 2015 (acoustic ID 24752) and May 19, 2015 (acoustic ID 24750) (Table 2). Female 24750 was

subsequently detected at rkm 146.4 on May 20th, 2015 based on her radio tag (radio ID 36). This is an interesting detection because it is approximately 8 rkm upstream of the known spawn location in Nechako River, and during an appropriate time for spawning. That female was detected in the VPS array on May 20. The other female was not detected upstream of the VPS array.

Two mature/flowing males and four immature males were released between April 14th and May 17th, 2015. One mature male and two immature males arrived at the VPS array/spawning reach between May 11th and 15th, several days before the ripe females arrived at the VPS. One immature male did not arrive at the VPS until June 3rd, one mature male did not arrive until June 23rd and one immature male did not arrive until July 21st. All radio detections of males occurred downstream of the VPS.

Last detection dates show that most males continue to visit the spawning reach for ~3-4 weeks, but the males that appear to arrive after the

Two acoustically tagged ripe females that were at large during spawning period were not detected. One of those females was released on May 19, at the beginning of the spawning period. There are several explanations for these “missing” spawners. Perhaps those females were unable to spawn in 2015 due to capture and tagging effects, or perhaps all of the acoustic receivers failed to detect those spawners while they were in the spawning reach. Another possibility includes the spawner fish spawned in areas downstream of the

Acoustic Telemetry - Spatial Distribution of White Sturgeons within VPS Array

Figure 8 displays all relocations calculated for each of the 8 fish identified in the filtered data. Different levels of detection are the majority of the data is derived from three males.

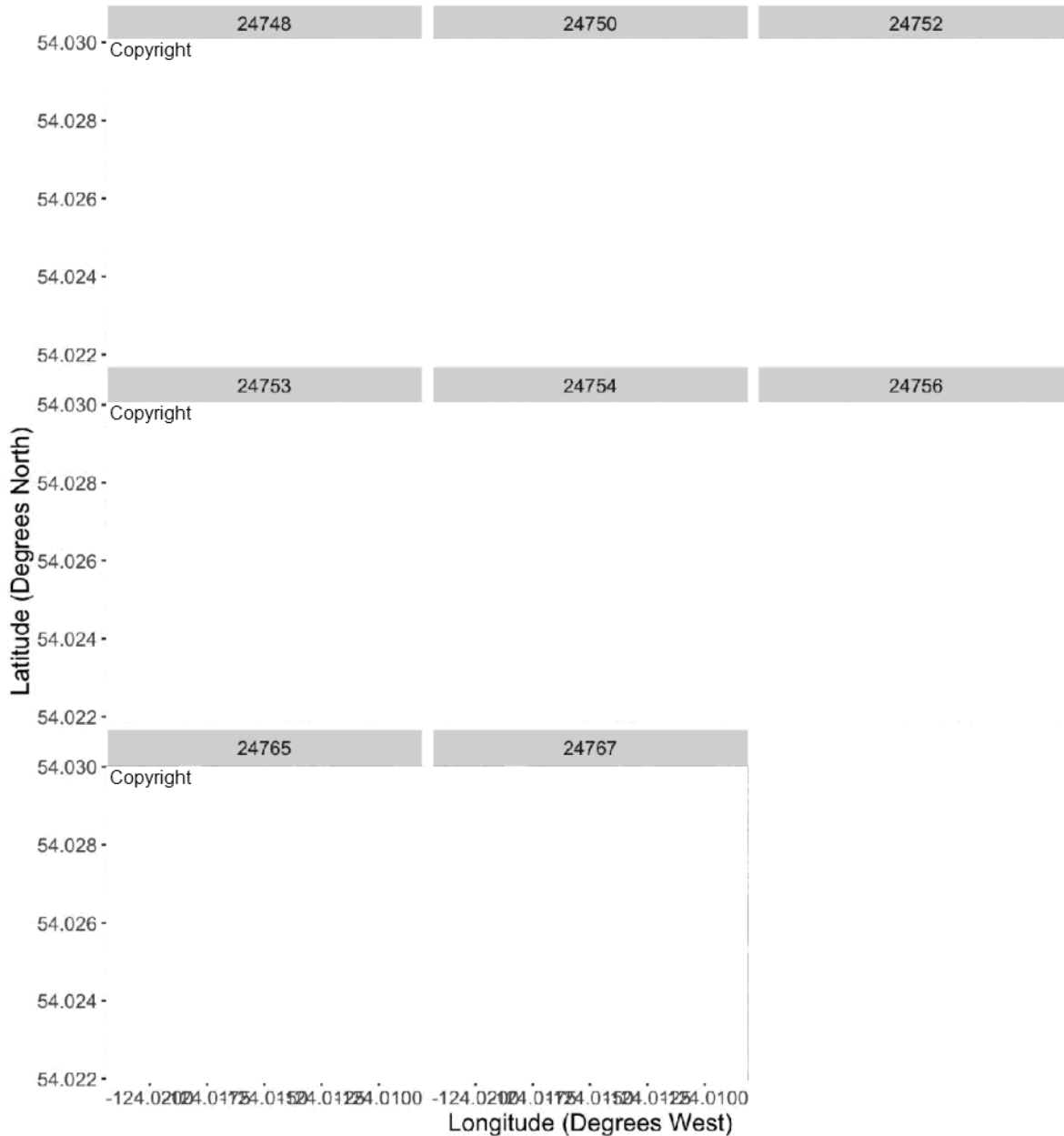


Figure 8. Each panel shows the entire relocation dataset for each acoustically tagged white sturgeon included in the filtered dataset (acoustic tag ID in grey panel-header). The gravel deposit is outlined in white.

Evaluation of position data suggests that fish were selectively utilizing the area of the lower pad. Habitat use (acoustic detections at a position within the detection zone) and habitat availability (i.e. areas in the detection zone were considered remediated (lower pad) or not remediated) were calculated and Manly's habitat selection test for constant resources was used to determine if fish were occupying the lower pad area more often than chance

(Desbiez, et al. 2009). The remediated lower pad area represents 14% of the available area within the detection zone, and the tagged white sturgeon had 31% of their relocations over the lower pad which suggests that white sturgeon were selectively using the area of the lower pad ($Khi2L = 1333.072$, $p < 0.000$, $W_i = 2.139$). Given that the majority of detections result from three individuals (one mature male and two immature males) this assessment does have the potential for some bias. For instance, the only two female trajectories show that most detections of female 24750 occur upstream of the gravel pad, whereas about half the detections for female 24752 occur within the area of the gravel pad.

Acoustic Telemetry - Sturgeon Trajectories

All calculated locations for each sturgeon were organized by time of detection to create a trajectory of movement for each sturgeon (Tables 4 and 5). Three males arrived at the VPS between May 11th and May 15th. These three males generated the largest trajectories. The other three males arrived on June 3rd, June 23rd, and July 21st, and had relatively small trajectories.

Two mature females arrived in the VPS on May 18th and May 19th. One female's last acoustic detection was shortly after on May 20th, and the other female's last detection was June 15th. Both of the female trajectories are relatively small, but may provide the most information on spawn site selection. Their trajectories are concentrated around May 19th and 20th, which is the same time as a confirmed spawn event (see egg mat results).

It was anticipated that the high frequency ping rate of the acoustic tags (40 – 80 seconds random delay) would enable high resolution temporal perspective of sturgeon movements within the spawning reach, and possibly use differences in selected statistics to classify behaviour types (see McLean et al. 2014). Unfortunately after filtering data to maintain position accuracy the mean time-step between relocations within a trajectory is approximately 112 seconds; too long to identify short duration movement patterns associated with spawning in sturgeon

Trajectories for individual fish detections were grouped (based on the definition below) to better understand the movement patterns within an individual. Each group of relocations is referred to as a trajectory burst. Bursts were defined as separate events when there was 10 minutes (600 seconds) between two neighboring relocations in the full trajectory. Using this

10-minute criterion created 286 bursts. One male sturgeon (Acoustic ID 24754) accounted for 207 of those bursts (Table 5 in Appendix A). Note that some bursts were deleted from the data set because they contained two or less relocations. Figures are divided into daily panels to visualize when trajectory bursts occurred in time.

Acoustic ID 24748, a mature male white sturgeon, showed a lot of activity in the VPS detection zone between May 18th and May 20th (a confirmed spawning period). This sturgeon clearly occupied the entire detection zone area, both over lower pad and areas both adjacent to and upstream of the lower pad. The ubiquitous habitat occupancy trajectory bursts are typical of other VPS-tracked male white sturgeon in this report.

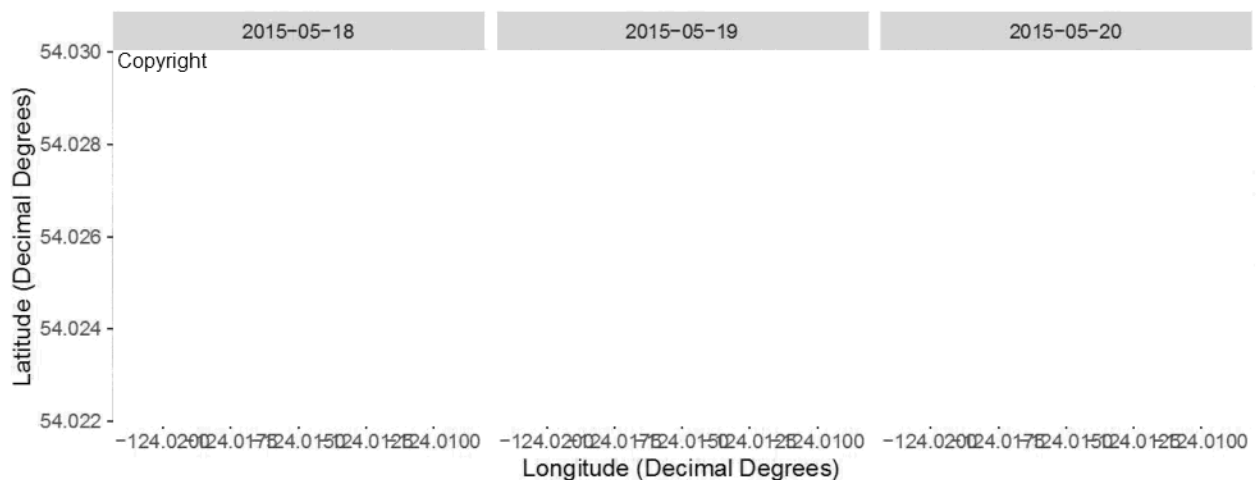


Figure 9. Nechako River white sturgeon (acoustic ID 24748, Male) trajectory bursts divided into days during the spawning period.

Acoustic ID 24750, a ripe female white sturgeon only had two trajectory bursts during the largest confirmed spawning event. One burst was slow moving and entirely upstream of the lower pad, and the other was a quick movement through the Murray Creek confluence and lower pad/thalweg. An assumed female spawning movement within a burst would have several relocations in close proximity because we assume the female inspects the site and then spawns there, which could take several minutes.

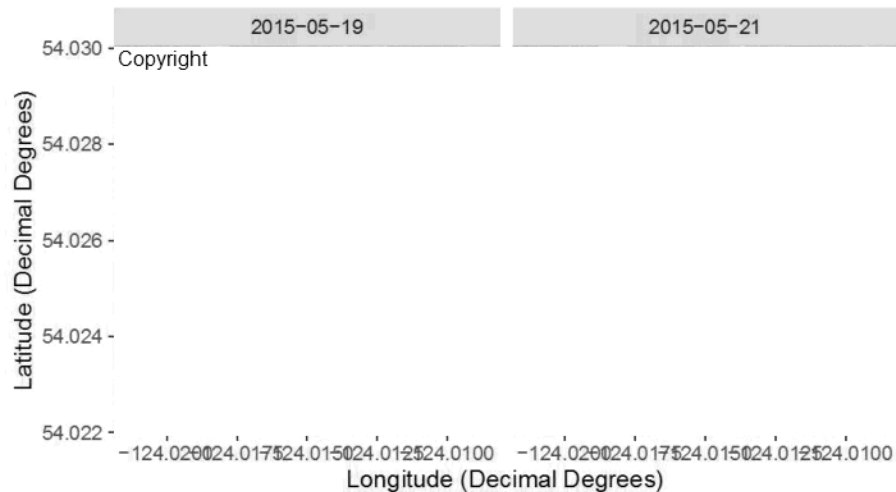


Figure 10. Nechako River white sturgeon (acoustic ID 24750, Female) trajectory bursts divided between days during a spawning event in 2015.

Acoustic ID 24752, a mature female white sturgeon recorded six trajectory bursts during the largest spawning event in 2015 (her entire trajectory). All of the bursts contained positions in the cobble zone. Bursts on May 18th and May 20th were short duration, but four bursts on May 19th are relatively long. All bursts from acoustic ID 24752 on May 19th occupy the center-southern edge of the lower pad for longer durations than other positions in the same burst. The trajectory bursts on May 19th could represent site selection and spawning behaviour in adult female white sturgeons because they possess all anticipated characteristics of spawning site selection in white sturgeon. Although there are a number of relocations over the lower pad, there are also a substantial number of relocations outside of the lower pad. Simply due to their timing within the spawning period they may also represent spawning events. Female 24752 bursts suggest spawning events occur both within and outside of the lower pad boundaries.

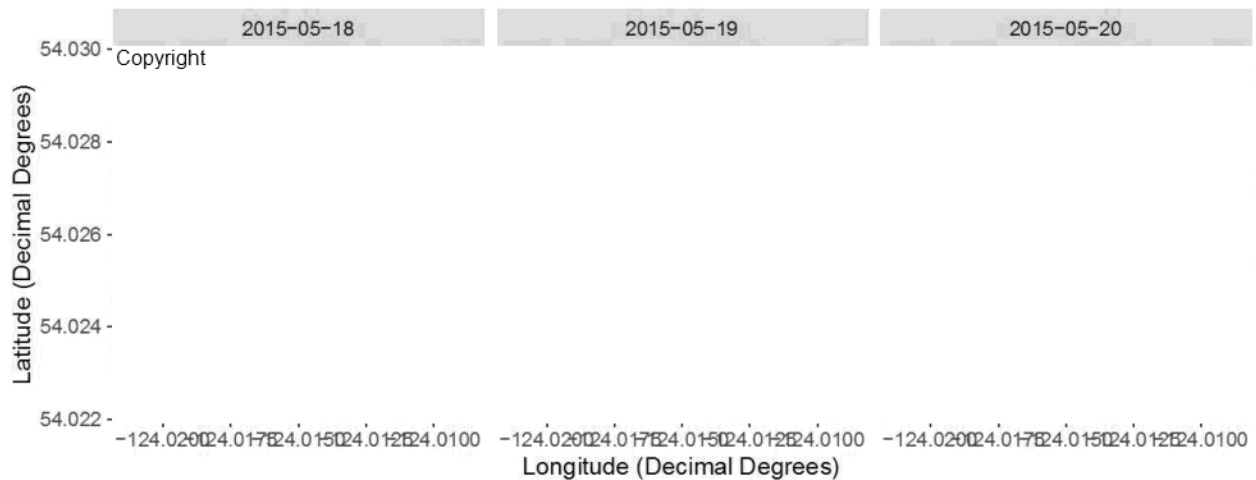


Figure 11. Nechako River white sturgeon (acoustic ID 24752, Female) trajectory bursts divided between days during a spawning event in 2015.

Acoustic ID 24754, an immature male adult white sturgeon had the largest trajectory of all the fish tracked in 2015. The spawning time bursts show ubiquitous habitat occupancy in the detection zone on all days, perhaps with a small preference over the cobble zone/thalweg. Note one trajectory burst from July 21st is provided as a reference for more “typical” daily activity outside an apparent spawning event (how do you know it isn’t spawning if there were not egg mats deployed?).

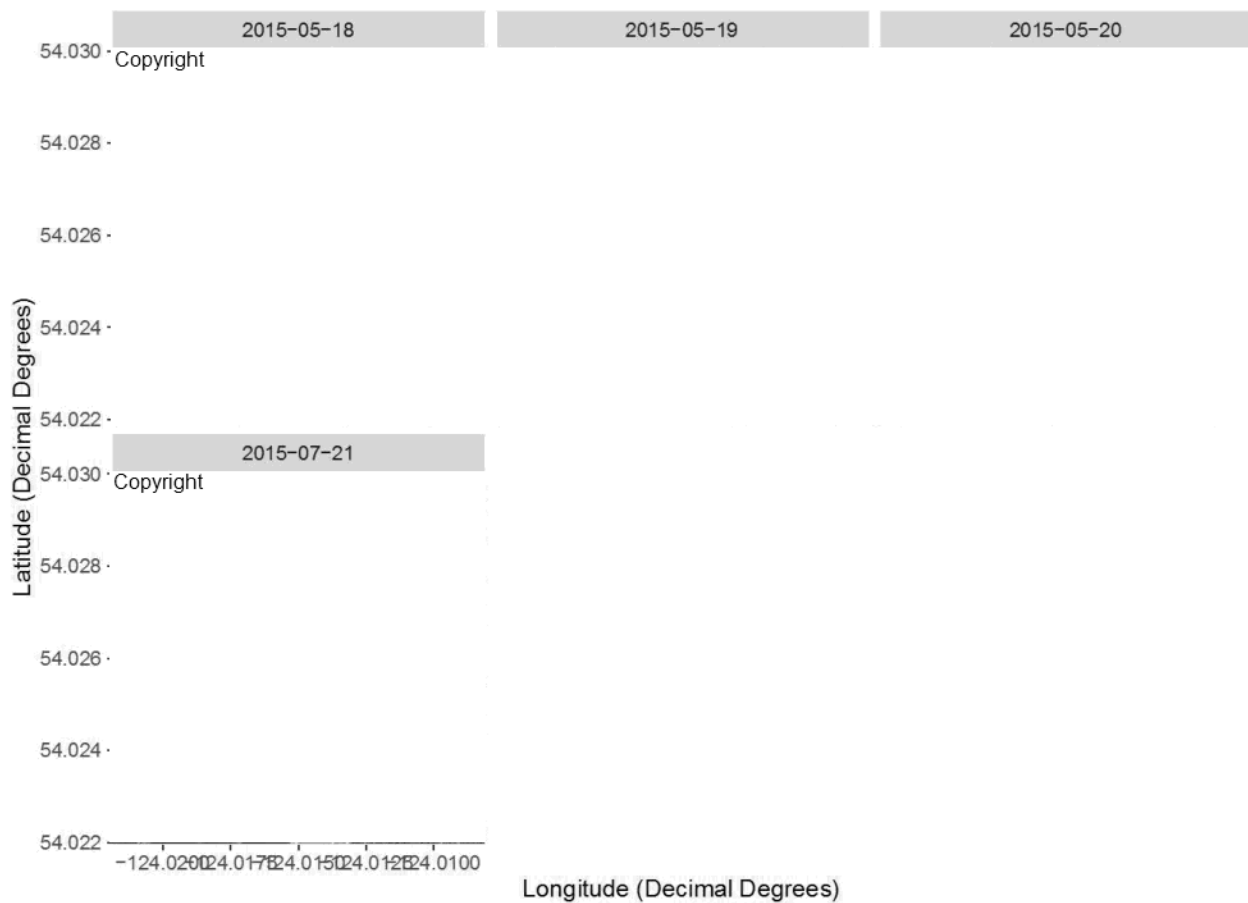


Figure 12. Nechako River white sturgeon (acoustic ID 24754, Male) trajectory bursts divided between days during a spawning event in 2015.

Acoustic ID 24756, an immature male adult white sturgeon also showed ubiquitous habitat occupancy during the large spawning event in 2015. On May 20th there does appear to be a slight preference for the cobble zone, although there are positions just upstream of the cobble zone that are repeatedly occupied. No assumptions were made on male white sturgeon spawning behaviour but results from this VPS study suggest all males show very active exploring/wandering movements within the detection zone.

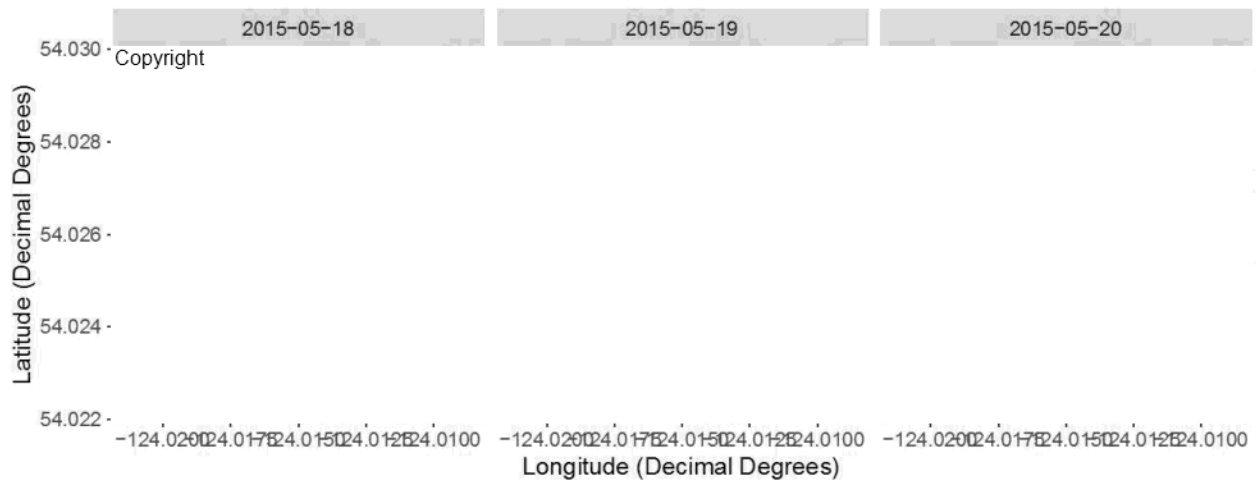


Figure 13. Nechako River white sturgeon (acoustic ID 24756, Male) trajectory bursts divided between days during a spawning event in 2015.

Conclusions

Spawn monitoring in 2015 included adult capture and tagging, egg detections within the spawning reach, radio telemetry pre-spawn and during spawn, and acoustic telemetry during spawn. Adult capture data show the white sturgeon are typically holding in locations between rkm 115 and rkm 135 pre-spawn. Radio detections and egg detections provided the basis for timing of spawning period, and confirmation of spawning events in previous years. In 2015 both radio telemetry and egg detections suggest the spawning period occurred between May 19th and May 23rd, 2015. Acoustic telemetry detections within the spawning reach show the greatest number of unique sturgeon, and the greatest number of daily detections on May 20th and 21st, which corroborate radio telemetry and egg detection results. Acoustic detections also provided fine-scale spatial movements of adult white sturgeon within the spawning reach, both during outside of spawn timing. The purpose of including a VPS array was to assess whether spawning activity was occurring over remediated areas, and to identify fine-scale spawning site selection. To assess spawning activity it is necessary to identify spawning-specific behaviours in the trajectory datasets. In our filtered trajectories (filtered for position error < 3.3m) the average time-lag between relocations was 112 seconds. Unfortunately this temporal resolution is too coarse to identify spawning-specific behaviours such as tail thrashing and small, quick acceleration bursts. The goal of accurately identifying spawning activity, and

thus spawning locations appears unlikely. Despite the temporal limitation, the trajectory dataset still accurately records fine-scale spatial data. The VPS data does provide the first evidence that tagged sturgeon are located over the remediated area a significant amount of time during spawning period. It is unclear why white sturgeon spent a significant amount of time over the remediated area. It is likely due to flow patterns in that particular area. Although there is plenty of activity over the remediated area the result may be slightly biased from non-spawning activity likely included in the three most active fish (males). None-the-less a general conclusion that white sturgeon are occupying the remediated area a significant amount during spawning period helps inform the next habitat recovery effort. Additional conclusions include a significant presence of non-mature male sturgeon in the spawning aggregation, and their arrival in the spawning reach four or five days earlier than mature females. Females only remained in the vicinity of the spawning sites for several days. The males that arrived before or during the spawning period continued to visit the spawning site for 3-4 weeks. Males that did not arrive until after the spawning period stayed for less time. While all recorded movements in the spawning reach during spawning period can provide valuable information on the variety of behaviours during spawning period, specific bursts of activity might be more informative on spawning site locations. Trajectory bursts recorded from females may be more informative than males since female residency in the area appears to be focused during periods of egg depositing, whereas trajectory bursts for males include the apparent arrival prior to females, movements by immature males, and movements outside of the apparent spawning period. Trajectory bursts detected from female sturgeon 24752 on May 20, 2015 may provide evidence for spawning site selection over the remediated area within the VPS detection zone. Spatial patterns in movement trajectories indicate that fish use areas within and outside of the area of the lower pad. Considering either overall movements for all fish or the restricted movements of the two females that may be more indicative of actual spawning events both suggest that some spawning activity also occurs outside of the current spawning pad locations. If this is consistently demonstrated under other flow conditions/years then future habitat restoration may need to consider a greater restoring a greater area of habitat. Additionally, some spawning does appear to be located within the current pads, which is

confirmed by egg detections. As such the location selected for the lower pad appears to be suitable (despite the continuing limitations caused by substrate conditions at that site – see NHC 2013)

Increasing the area covered by VPS will show how much sturgeon activity occurs outside of the 2015 detection zone. An “upper” gravel pad, upstream of the one monitored in 2015, was also installed, and should be monitored. Increasing the area covered by VPS could also provide context for spawning site boundaries. Since it appears temporal-resolution of detections may limit super-fine scale classification of spawning behaviours, decreasing the density of acoustic receivers will not compromise the VPS array functionality. In addition, low water years will have a reduced area to cover and current receiver inventory can cover more area.

White sturgeon appear to prefer particular zones within the spawning reach, depending on flow conditions. In high flow years (such as 2015) egg detections are more abundant in the single thread channel area 500m up and downstream of Burrard Bridge (including the lower pad and VPS detection zone) (unpublished data). In lower flow years egg detections are more abundant within the main braided channel and island complex, including Stoney River confluence and upper pad site. 2015 was a year we would expect small amounts of sedimentation at the lower site, and greater amounts of sedimentation in the upper site due to back-watering effects in that area given high flow conditions. This year was also an ideal year to focus monitoring efforts at the lower site due to sturgeons preference for the lower site area in high flow years. However in low flow years the same VPS array deployment may not be as successful in detection sturgeon spawning activity. Each year the monitoring effort must be customized to match expected habitat occupancy based on conditions. It is unclear if the abundance of egg detections downstream of Burrard Bridge on high flow years is a result of a greater proportion of spawning events occurring in that area, or a result of flow dynamics in that area relative to other areas in the spawning reach. It is likely both factors are shaping the apparent preference.

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Appendix A : Tables

Table 1. Summary of all adult shite sturgeon captured and tagged during 2015 monitoring efforts.

PIT ID	Total Length (cm)	Maturity Code	Fate	Capture Date	Capture rKm	Release Date	Release rKm	Tags at Release
41247A5430	206.2	3	Released	15-04-21	116.8	15-04-21	116.8	Pit Radio Acoustic
7F7D7C115E	224.9	4	Released	15-04-23	110.7	15-04-23	110.7	Pit Radio Acoustic
7F7B031A21	242.1	12	Released	15-04-23	116.0	15-04-23	116.0	Pit Radio
401D52192D	224.5	5	Released	15-04-28	125.3	15-04-28	125.3	Pit Radio Acoustic
41250B2C18	244.0	4	Released	15-05-01	121.3	15-05-01	121.3	Pit Radio Acoustic
4527573D3F	253.8	3	Released	15-05-05	125.1	15-05-05	125.1	Pit Radio Acoustic
2224172A7D	210.3	15	Released	15-05-05	129.9	15-05-05	129.9	Pit Radio Acoustic
7F7D7A6A66	238.0	3	Released	15-05-07	129.2	15-05-07	129.2	Pit Radio Acoustic
152217662A	283.5	15	Released	15-05-14	132.7	15-05-14	132.7	Pit Radio Acoustic
7F7B0C6725	208.2	3	Released	15-05-14	129.2	15-05-14	129.2	Pit Radio Acoustic
7F7B031A21	NA	12	Released	15-05-15	129.8	15-05-15	129.8	Pit Radio
7F7D7D2657	236.0	11	Released	15-05-16	127.6	15-05-16	125.6	Pit Radio
45247E083C	240.5	3	Released	15-05-17	127.6	15-05-17	127.6	Pit Radio Acoustic
424F046D54	234.1	15	Released	15-05-17	130.7	15-05-17	NA	Pit Radio Acoustic
			Brood					
41250F5929	238.0	15	Unused	15-05-05	127.6	15-05-19	135.3	Pit Radio Acoustic
4529173846	203.2	12	Released	15-05-20	129.3	15-05-20	129.3	Pit Radio
41247A5430	NA	3	Released	15-05-20	133.8	15-05-20	133.8	Pit Radio
7F7B0B2E51	220.7	3	Released	15-05-21	137.1	15-05-21	137.1	Pit Radio Acoustic
7F7B031A21	NA	12	Released	15-05-23	130.1	15-05-22	130.1	
152219662A	252.5	15	Brood	15-04-21	110.7	15-05-26	130.1	Pit Radio
6C00072572	272.5	15	Brood	15-04-23	116.9	15-05-26	130.1	Pit Radio
6C00072550	261.5	15	Brood	15-05-15	127.6	15-05-26	130.1	Pit Radio
45286C6E35	219.0	5	Brood	15-04-14	117.7	15-06-02	130.1	Pit Radio Acoustic
45284E7344	227.3	5	Brood	15-05-07	128.0	15-06-02	130.1	Pit Radio Acoustic
6C00072535	262.0	15	Brood	15-05-12	132.5	15-06-02	130.1	Pit Radio
6C00072608	245.0	5	Brood	15-05-13	132.7	15-06-02	130.1	Pit Radio Acoustic
6C00072610	277.0	15	Brood	15-05-17	134.4	15-06-02	130.0	Pit Radio
7F7B033461	230.0	4	Brood	15-04-30	130.5	15-06-02	130.1	Pit Radio Acoustic
7F7D7C631A	204.5	3	Brood	15-04-21	110.7	15-06-02	130.1	Pit Radio
			Brood					
7F7D781A4D	221.7	13	Held	15-04-14	117.7			

Table 2. Number of positions calculated for each stationary sync tag over the entire VPS deployment. Percent of total possible positions is calculated based on an average ping frequency of the sync tags over the deployment period.

Sync Tag ID	Stn 01	Stn 02	Stn 03	Stn 04	Stn 05	Stn 06	Stn 07	Stn 08	Stn 09	Stn 10	Stn 11	Stn 12	Stn 13	Stn 14	Stn 15	Stn 16	Stn 17	Stn 18	Average
Positioning Percentage (%)	79.94	82.36	74.79	81.9	83.71	81.46	68.82	81.67	85.26	85.42	83.7	72.26	74.12	88.98	86.04	55.97	12.61	29.31	72.68

Table 3. Biological and telemetry data for eight white sturgeon remaining after HPE < 10 filter applied to VPS data. White sturgeon were released at their capture site.

Sex	Acoustic ID	Radio ID	Radio Frequency (mhz)	Total Length (cm)	Maturity	Capture rkm	Release Date	Radio Detection rkm Range
F	24752	37	148.600	210.3	Ripe (15)	129.9	2015-05-05	134
F	24750	36	148.600	283.5	Ripe (15)	132.7	2015-05-14	133.3 - 146.4
M	24765	54	148.600	219.0	Mature (4)	117.7	2015-05-14	NA
M	24748	39	148.600	224.5	Flowing (5)	125.3	2015-04-28	127.8 - 135.7
M	24754	52	149.520	253.8	Immature (3)	125.1	2015-05-05	110.5 - 135.4
M	24756	38	148.600	238.0	Immature (3)	129.2	2015-05-07	132.1 – 135.7
M	24767	52	148.600	245.0	Immature (3)	132.7	2015-05-13	NA
M	24753	28	148.600	240.5	Immature (3)	127.6	2015-05-17	NA

Table 4. Detection summary of white sturgeon that produced trajectories during 2015 VPS spawn monitoring.

Sex	Acoustic ID	Number of Detections	First Detection Date (UTC)	First Detection Time (UTC)	Last Detection Date (UTC)	Last Detection Time (UTC)
M	24748	1173	2015-05-11	04:15:10	2015-06-05	12:27:02
F	24750	57	2015-05-19	04:18:30	2015-06-15	19:55:04
F	24752	51	2015-05-18	13:23:14	2015-05-20	15:23:28
M	24753	15	2015-07-21	11:58:56	2015-07-21	12:15:24
M	24754	4660	2015-05-13	06:59:54	2015-07-21	19:52:27
M	24756	1668	2015-05-15	09:41:17	2015-06-04	12:29:03
M	24765	38	2015-06-23	22:51:50	2015-06-30	02:54:38
M	24767	32	2015-06-03	00:17:54	2015-07-14	20:47:14

Table 5. Summary of Nechako River white sturgeon burst trajectories recorded during 2015 spawning season.

Acoustic ID	Burst ID	Number of Relocations	Start Date (UTC)	Start Time (UTC)	End Date (UTC)	End Time (UTC)
24748	24748.01	4	2015-05-11	04:15:10	2015-05-11	04:20:38
24748	24748.02	8	2015-05-11	10:37:17	2015-05-11	10:52:42
24748	24748.03	19	2015-05-18	14:52:56	2015-05-18	15:19:27
24748	24748.04	4	2015-05-18	15:29:41	2015-05-18	15:41:20
24748	24748.05	44	2015-05-18	17:51:34	2015-05-18	19:18:24
24748	24748.06	18	2015-05-18	19:51:23	2015-05-18	20:31:01
24748	24748.07	20	2015-05-18	22:31:48	2015-05-18	23:07:39
24748	24748.08	23	2015-05-18	23:24:51	2015-05-19	00:01:08
24748	24748.01	19	2015-05-19	02:11:49	2015-05-19	02:44:53
24748	24748.12	9	2015-05-19	03:12:18	2015-05-19	03:37:47
24748	24748.14	76	2015-05-19	04:05:13	2015-05-19	06:43:57
24748	24748.15	11	2015-05-19	06:55:07	2015-05-19	07:13:43
24748	24748.16	29	2015-05-19	08:17:48	2015-05-19	09:11:47
24748	24748.17	48	2015-05-19	09:23:38	2015-05-19	11:29:33
24748	24748.19	17	2015-05-19	12:50:15	2015-05-19	13:24:48
24748	24748.02	42	2015-05-19	13:39:39	2015-05-19	14:55:23
24748	24748.21	42	2015-05-19	15:13:27	2015-05-19	17:17:37
24748	24748.22	11	2015-05-19	17:28:54	2015-05-19	17:50:21
24748	24748.24	16	2015-05-19	18:17:06	2015-05-19	18:46:19
24748	24748.25	9	2015-05-19	18:58:00	2015-05-19	19:18:45
24748	24748.26	11	2015-05-19	19:52:08	2015-05-19	20:16:31
24748	24748.27	49	2015-05-19	20:50:43	2015-05-19	22:36:14
24748	24748.28	59	2015-05-19	22:55:33	2015-05-20	00:43:51
24748	24748.29	21	2015-05-20	01:35:11	2015-05-20	02:08:57
24748	24748.03	58	2015-05-20	02:32:49	2015-05-20	04:04:08
24748	24748.32	47	2015-05-20	05:09:56	2015-05-20	06:26:57
24748	24748.33	19	2015-05-20	06:37:19	2015-05-20	07:13:02
24748	24748.34	59	2015-05-20	07:23:41	2015-05-20	09:19:35
24748	24748.35	63	2015-05-20	09:30:26	2015-05-20	11:26:33
24748	24748.36	9	2015-05-20	11:38:49	2015-05-20	11:52:09
24748	24748.37	85	2015-05-20	12:03:31	2015-05-20	14:48:52
24748	24748.38	44	2015-05-20	15:55:50	2015-05-20	17:15:13
24748	24748.39	120	2015-05-20	17:28:59	2015-05-20	21:11:42
24748	24748.04	6	2015-05-22	13:00:27	2015-05-22	13:05:36
24748	24748.41	14	2015-05-27	14:10:57	2015-05-27	14:31:32
24748	24748.42	3	2015-06-01	00:51:50	2015-06-01	00:54:34
24748	24748.43	8	2015-06-01	08:17:57	2015-06-01	08:28:53
24748	24748.44	3	2015-06-01	10:43:56	2015-06-01	10:46:02
24748	24748.45	9	2015-06-02	14:32:50	2015-06-02	14:42:53
24748	24748.46	6	2015-06-05	12:20:43	2015-06-05	12:27:02
24750	24750.1	10	2015-05-19	04:18:30	2015-05-19	04:28:14
24750	24750.2	7	2015-05-21	06:09:16	2015-05-21	06:15:56

24750	24750.3	6	2015-05-22	16:17:37	2015-05-22	16:27:03
24750	24750.4	19	2015-05-24	12:35:27	2015-05-24	13:02:51
24750	24750.5	14	2015-05-26	01:25:44	2015-05-26	01:39:28
24752	24752.1	5	2015-05-18	13:23:14	2015-05-18	13:28:02
24752	24752.2	11	2015-05-19	08:36:30	2015-05-19	08:53:44
24752	24752.3	12	2015-05-19	09:05:57	2015-05-19	09:20:14
24752	24752.4	11	2015-05-19	09:31:33	2015-05-19	09:51:50
24752	24752.6	4	2015-05-19	15:08:19	2015-05-19	15:16:39
24752	24752.7	7	2015-05-20	15:15:11	2015-05-20	15:23:28
24753	24753.1	15	2015-07-21	11:58:56	2015-07-21	12:15:24
24754	24754.001	20	2015-05-13	06:59:54	2015-05-13	07:30:49
24754	24754.002	19	2015-05-13	08:54:06	2015-05-13	09:22:33
24754	24754.003	5	2015-05-13	09:39:07	2015-05-13	09:44:02
24754	24754.004	34	2015-05-13	09:54:38	2015-05-13	10:49:41
24754	24754.005	7	2015-05-13	11:14:13	2015-05-13	11:24:46
24754	24754.006	7	2015-05-13	12:21:00	2015-05-13	12:29:07
24754	24754.007	33	2015-05-14	07:21:48	2015-05-14	08:14:11
24754	24754.008	48	2015-05-15	06:31:18	2015-05-15	07:33:27
24754	24754.009	65	2015-05-15	07:44:45	2015-05-15	09:33:06
24754	24754.010	45	2015-05-15	09:45:45	2015-05-15	11:28:42
24754	24754.011	6	2015-05-15	13:14:38	2015-05-15	13:29:16
24754	24754.012	44	2015-05-15	13:39:49	2015-05-15	14:42:20
24754	24754.013	22	2015-05-15	14:59:55	2015-05-15	15:33:00
24754	24754.014	42	2015-05-18	14:45:25	2015-05-18	16:29:02
24754	24754.015	27	2015-05-18	16:44:20	2015-05-18	17:59:17
24754	24754.016	36	2015-05-18	18:21:39	2015-05-18	19:34:45
24754	24754.017	44	2015-05-19	00:11:03	2015-05-19	01:12:02
24754	24754.018	18	2015-05-19	01:33:23	2015-05-19	01:54:32
24754	24754.020	9	2015-05-19	04:15:46	2015-05-19	04:38:39
24754	24754.021	66	2015-05-19	04:48:49	2015-05-19	07:13:24
24754	24754.022	78	2015-05-19	08:18:30	2015-05-19	11:29:45
24754	24754.023	15	2015-05-19	11:42:12	2015-05-19	12:05:32
24754	24754.024	53	2015-05-19	12:26:43	2015-05-19	14:19:25
24754	24754.025	3	2015-05-19	14:29:48	2015-05-19	14:36:01
24754	24754.026	102	2015-05-19	14:54:05	2015-05-19	18:43:36
24754	24754.027	9	2015-05-19	18:56:05	2015-05-19	19:17:19
24754	24754.028	12	2015-05-19	19:27:57	2015-05-19	19:44:20
24754	24754.029	11	2015-05-19	20:00:19	2015-05-19	20:30:58
24754	24754.030	67	2015-05-19	20:43:31	2015-05-19	22:51:14
24754	24754.031	124	2015-05-19	23:02:40	2015-05-20	02:25:26
24754	24754.032	21	2015-05-20	03:24:00	2015-05-20	03:56:12
24754	24754.033	13	2015-05-20	04:27:30	2015-05-20	04:51:00
24754	24754.034	3	2015-05-20	05:02:43	2015-05-20	05:06:01
24754	24754.035	19	2015-05-20	05:32:18	2015-05-20	05:57:20
24754	24754.036	3	2015-05-20	06:13:08	2015-05-20	06:23:38
24754	24754.039	7	2015-05-20	07:20:13	2015-05-20	07:47:30
24754	24754.040	7	2015-05-20	08:06:57	2015-05-20	08:22:50

24754	24754.041	12	2015-05-20	08:34:58	2015-05-20	08:58:13
24754	24754.042	42	2015-05-20	09:13:06	2015-05-20	10:36:23
24754	24754.043	14	2015-05-20	10:46:46	2015-05-20	11:17:55
24754	24754.044	17	2015-05-20	11:36:32	2015-05-20	12:06:42
24754	24754.045	8	2015-05-20	12:24:48	2015-05-20	12:41:48
24754	24754.046	27	2015-05-20	12:56:15	2015-05-20	13:31:10
24754	24754.047	5	2015-05-20	14:19:29	2015-05-20	14:28:14
24754	24754.048	7	2015-05-23	05:43:53	2015-05-23	05:53:29
24754	24754.050	10	2015-05-23	07:43:19	2015-05-23	07:53:36
24754	24754.051	20	2015-05-25	14:55:55	2015-05-25	15:34:45
24754	24754.052	12	2015-05-25	16:05:54	2015-05-25	16:18:03
24754	24754.053	3	2015-05-25	16:47:09	2015-05-25	16:49:48
24754	24754.055	38	2015-05-25	17:23:58	2015-05-25	18:06:42
24754	24754.056	26	2015-05-25	18:17:23	2015-05-25	18:57:18
24754	24754.057	50	2015-05-25	19:08:33	2015-05-25	20:33:50
24754	24754.058	8	2015-05-25	22:44:54	2015-05-25	22:53:51
24754	24754.059	8	2015-05-25	23:45:35	2015-05-25	23:57:10
24754	24754.060	18	2015-05-26	00:32:42	2015-05-26	00:50:54
24754	24754.061	4	2015-06-02	05:21:43	2015-06-02	05:25:10
24754	24754.062	75	2015-06-04	06:57:45	2015-06-04	08:46:14
24754	24754.064	11	2015-06-09	05:29:55	2015-06-09	05:48:49
24754	24754.065	5	2015-06-09	17:06:26	2015-06-09	17:11:14
24754	24754.066	7	2015-06-09	23:46:57	2015-06-09	23:54:48
24754	24754.067	10	2015-06-10	01:50:25	2015-06-10	02:06:41
24754	24754.068	15	2015-06-10	02:17:46	2015-06-10	02:38:17
24754	24754.069	3	2015-06-10	03:01:55	2015-06-10	03:03:49
24754	24754.070	14	2015-06-10	04:36:13	2015-06-10	05:05:46
24754	24754.071	37	2015-06-10	06:25:57	2015-06-10	07:17:05
24754	24754.072	9	2015-06-10	07:34:45	2015-06-10	07:43:43
24754	24754.073	4	2015-06-10	08:34:42	2015-06-10	08:43:57
24754	24754.074	3	2015-06-10	09:07:08	2015-06-10	09:12:23
24754	24754.075	41	2015-06-10	12:00:18	2015-06-10	13:07:43
24754	24754.076	19	2015-06-10	14:06:26	2015-06-10	14:44:58
24754	24754.077	40	2015-06-10	15:32:58	2015-06-10	16:33:53
24754	24754.078	15	2015-06-10	17:14:02	2015-06-10	17:35:59
24754	24754.079	32	2015-06-10	18:38:43	2015-06-10	19:25:10
24754	24754.080	8	2015-06-10	19:46:35	2015-06-10	20:08:29
24754	24754.081	15	2015-06-10	20:19:06	2015-06-10	20:37:21
24754	24754.082	24	2015-06-10	21:15:21	2015-06-10	21:46:13
24754	24754.083	49	2015-06-10	21:58:09	2015-06-10	23:16:15
24754	24754.084	31	2015-06-10	23:30:10	2015-06-11	00:16:28
24754	24754.085	9	2015-06-11	00:48:18	2015-06-11	01:01:54
24754	24754.086	21	2015-06-26	18:27:26	2015-06-26	18:59:24
24754	24754.087	3	2015-06-26	19:18:21	2015-06-26	19:28:34
24754	24754.088	25	2015-06-26	19:52:09	2015-06-26	20:37:38
24754	24754.089	31	2015-06-26	22:42:55	2015-06-26	23:35:57
24754	24754.091	20	2015-06-27	01:06:17	2015-06-27	01:46:32

24754	24754.093	12	2015-06-27	02:41:23	2015-06-27	03:02:57
24754	24754.094	24	2015-06-27	04:51:26	2015-06-27	05:42:24
24754	24754.097	5	2015-06-27	07:05:00	2015-06-27	07:13:14
24754	24754.099	29	2015-06-28	04:40:50	2015-06-28	05:31:28
24754	24754.100	22	2015-06-28	07:54:02	2015-06-28	08:35:41
24754	24754.101	15	2015-06-28	09:04:12	2015-06-28	09:20:50
24754	24754.102	10	2015-06-28	09:46:35	2015-06-28	09:59:12
24754	24754.103	32	2015-06-28	11:06:32	2015-06-28	11:56:21
24754	24754.104	11	2015-06-28	13:05:41	2015-06-28	13:20:43
24754	24754.105	12	2015-06-28	13:34:42	2015-06-28	13:51:41
24754	24754.107	11	2015-06-28	15:38:40	2015-06-28	15:58:49
24754	24754.108	5	2015-06-28	16:19:48	2015-06-28	16:27:07
24754	24754.109	20	2015-06-28	16:40:59	2015-06-28	17:06:49
24754	24754.110	51	2015-06-28	19:04:42	2015-06-28	20:28:29
24754	24754.111	27	2015-06-28	20:56:49	2015-06-28	21:29:32
24754	24754.112	59	2015-06-28	21:40:07	2015-06-28	23:29:01
24754	24754.113	13	2015-06-29	00:28:06	2015-06-29	00:48:22
24754	24754.114	7	2015-06-29	01:14:47	2015-06-29	01:38:38
24754	24754.115	22	2015-06-29	01:48:50	2015-06-29	02:34:38
24754	24754.116	6	2015-06-29	03:09:57	2015-06-29	03:21:37
24754	24754.117	27	2015-06-29	03:46:53	2015-06-29	04:27:52
24754	24754.118	34	2015-06-29	04:43:43	2015-06-29	05:31:48
24754	24754.119	13	2015-06-29	05:58:41	2015-06-29	06:13:58
24754	24754.120	16	2015-06-29	09:42:41	2015-06-29	10:18:22
24754	24754.121	43	2015-06-29	11:27:26	2015-06-29	12:35:26
24754	24754.122	10	2015-06-29	12:48:06	2015-06-29	13:10:18
24754	24754.123	8	2015-06-29	13:48:33	2015-06-29	14:11:01
24754	24754.124	24	2015-06-29	14:27:11	2015-06-29	14:59:12
24754	24754.125	27	2015-06-29	16:32:13	2015-06-29	17:15:06
24754	24754.126	12	2015-06-29	18:18:13	2015-06-29	18:36:49
24754	24754.128	7	2015-06-29	19:50:31	2015-06-29	20:03:38
24754	24754.129	19	2015-06-29	21:06:34	2015-06-29	21:31:22
24754	24754.130	16	2015-06-29	22:14:36	2015-06-29	22:38:35
24754	24754.131	29	2015-06-29	23:44:36	2015-06-30	00:35:58
24754	24754.132	15	2015-06-30	02:18:11	2015-06-30	02:38:45
24754	24754.133	7	2015-06-30	02:56:01	2015-06-30	03:11:33
24754	24754.134	35	2015-06-30	03:53:33	2015-06-30	04:45:15
24754	24754.136	15	2015-06-30	08:54:33	2015-06-30	09:24:47
24754	24754.137	8	2015-06-30	11:27:35	2015-06-30	11:42:59
24754	24754.138	25	2015-06-30	11:58:35	2015-06-30	12:55:39
24754	24754.139	20	2015-06-30	13:11:19	2015-06-30	13:41:47
24754	24754.141	25	2015-06-30	14:11:16	2015-06-30	14:56:53
24754	24754.142	23	2015-06-30	16:02:21	2015-06-30	16:40:04
24754	24754.143	37	2015-06-30	17:00:47	2015-06-30	17:54:08
24754	24754.144	36	2015-06-30	18:26:02	2015-06-30	19:20:19
24754	24754.145	5	2015-06-30	19:30:37	2015-06-30	19:44:18
24754	24754.146	21	2015-06-30	19:59:43	2015-06-30	20:29:18

24754	24754.147	6	2015-06-30	20:46:52	2015-06-30	21:03:51
24754	24754.148	26	2015-06-30	22:14:23	2015-06-30	22:49:14
24754	24754.149	30	2015-06-30	23:26:04	2015-07-01	00:06:53
24754	24754.150	9	2015-07-01	00:41:59	2015-07-01	00:58:48
24754	24754.151	17	2015-07-01	02:55:28	2015-07-01	03:26:58
24754	24754.152	39	2015-07-01	03:48:56	2015-07-01	04:49:47
24754	24754.153	33	2015-07-01	06:55:26	2015-07-01	07:43:47
24754	24754.154	22	2015-07-01	08:06:11	2015-07-01	08:34:23
24754	24754.155	20	2015-07-01	09:32:41	2015-07-01	10:01:10
24754	24754.156	56	2015-07-01	11:41:31	2015-07-01	13:12:16
24754	24754.157	5	2015-07-01	13:36:26	2015-07-01	13:42:26
24754	24754.158	22	2015-07-01	13:52:31	2015-07-01	14:28:10
24754	24754.159	56	2015-07-01	16:07:31	2015-07-01	17:59:10
24754	24754.160	20	2015-07-01	19:04:46	2015-07-01	19:37:32
24754	24754.161	66	2015-07-01	20:40:24	2015-07-01	22:27:18
24754	24754.162	41	2015-07-01	22:46:39	2015-07-01	23:46:12
24754	24754.163	36	2015-07-02	00:06:08	2015-07-02	00:49:23
24754	24754.164	33	2015-07-02	08:03:44	2015-07-02	08:57:33
24754	24754.165	38	2015-07-02	09:53:34	2015-07-02	11:00:13
24754	24754.166	20	2015-07-02	11:23:48	2015-07-02	12:02:56
24754	24754.167	19	2015-07-02	12:27:08	2015-07-02	12:53:26
24754	24754.168	13	2015-07-02	13:38:58	2015-07-02	13:55:10
24754	24754.170	5	2015-07-02	16:49:24	2015-07-02	16:59:51
24754	24754.171	33	2015-07-02	17:59:30	2015-07-02	19:01:30
24754	24754.172	24	2015-07-02	20:10:40	2015-07-02	20:56:56
24754	24754.173	43	2015-07-02	22:40:12	2015-07-02	23:56:48
24754	24754.174	49	2015-07-03	00:54:43	2015-07-03	02:00:10
24754	24754.175	24	2015-07-03	04:27:21	2015-07-03	05:01:21
24754	24754.176	28	2015-07-03	06:03:20	2015-07-03	06:46:16
24754	24754.177	41	2015-07-03	07:46:22	2015-07-03	08:52:09
24754	24754.178	33	2015-07-03	10:59:09	2015-07-03	11:51:19
24754	24754.179	56	2015-07-03	13:58:57	2015-07-03	15:15:56
24754	24754.180	11	2015-07-03	18:05:13	2015-07-03	18:21:34
24754	24754.181	15	2015-07-03	19:08:29	2015-07-03	19:31:49
24754	24754.182	21	2015-07-04	06:08:05	2015-07-04	06:43:16
24754	24754.183	32	2015-07-04	10:06:43	2015-07-04	11:16:01
24754	24754.184	39	2015-07-04	12:12:54	2015-07-04	13:03:38
24754	24754.185	32	2015-07-04	13:16:15	2015-07-04	14:16:15
24754	24754.186	16	2015-07-04	16:07:17	2015-07-04	16:27:29
24754	24754.187	50	2015-07-04	16:41:26	2015-07-04	18:08:13
24754	24754.188	13	2015-07-04	21:42:22	2015-07-04	22:09:30
24754	24754.189	19	2015-07-05	00:11:26	2015-07-05	00:37:14
24754	24754.190	24	2015-07-05	05:52:48	2015-07-05	06:26:41
24754	24754.191	32	2015-07-05	07:41:25	2015-07-05	08:43:10
24754	24754.192	24	2015-07-05	12:12:53	2015-07-05	12:51:15
24754	24754.193	3	2015-07-05	13:33:11	2015-07-05	13:37:23
24754	24754.194	54	2015-07-05	13:49:28	2015-07-05	15:09:12

24754	24754.195	10	2015-07-05	15:23:38	2015-07-05	15:33:41
24754	24754.196	25	2015-07-05	16:02:13	2015-07-05	16:29:55
24754	24754.197	26	2015-07-05	18:35:21	2015-07-05	19:10:37
24754	24754.198	38	2015-07-05	19:43:54	2015-07-05	20:52:25
24754	24754.200	21	2015-07-05	21:40:22	2015-07-05	22:24:05
24754	24754.201	6	2015-07-05	22:43:56	2015-07-05	22:52:16
24754	24754.202	13	2015-07-05	23:12:56	2015-07-05	23:38:25
24754	24754.203	26	2015-07-06	00:41:09	2015-07-06	01:16:40
24754	24754.204	33	2015-07-06	02:04:11	2015-07-06	02:59:02
24754	24754.205	67	2015-07-06	04:13:26	2015-07-06	05:55:20
24754	24754.206	15	2015-07-21	17:35:24	2015-07-21	19:01:31
24754	24754.207	7	2015-07-21	19:22:29	2015-07-21	19:52:27
24756	24756.01	8	2015-05-15	09:41:17	2015-05-15	09:55:43
24756	24756.04	6	2015-05-18	07:52:13	2015-05-18	08:08:06
24756	24756.05	112	2015-05-18	09:04:18	2015-05-18	11:52:58
24756	24756.06	92	2015-05-18	13:46:10	2015-05-18	15:57:38
24756	24756.07	63	2015-05-18	16:08:04	2015-05-18	18:03:33
24756	24756.08	31	2015-05-18	18:15:03	2015-05-18	19:38:13
24756	24756.09	9	2015-05-18	19:59:16	2015-05-18	20:16:17
24756	24756.10	73	2015-05-18	23:05:35	2015-05-19	01:20:41
24756	24756.11	11	2015-05-19	01:33:34	2015-05-19	01:53:56
24756	24756.12	99	2015-05-19	04:15:50	2015-05-19	07:13:32
24756	24756.13	68	2015-05-19	08:18:46	2015-05-19	10:35:28
24756	24756.14	134	2015-05-19	10:46:35	2015-05-19	15:12:38
24756	24756.15	89	2015-05-19	15:25:52	2015-05-19	17:33:11
24756	24756.16	8	2015-05-19	17:44:55	2015-05-19	17:59:29
24756	24756.17	14	2015-05-19	18:10:02	2015-05-19	18:34:41
24756	24756.19	10	2015-05-19	18:57:33	2015-05-19	19:37:11
24756	24756.20	13	2015-05-19	20:06:59	2015-05-19	20:27:58
24756	24756.21	12	2015-05-19	20:38:51	2015-05-19	21:04:27
24756	24756.22	68	2015-05-19	21:14:31	2015-05-19	23:32:49
24756	24756.23	145	2015-05-20	00:00:03	2015-05-20	03:47:36
24756	24756.24	8	2015-05-20	04:23:12	2015-05-20	04:35:40
24756	24756.25	11	2015-05-20	04:49:01	2015-05-20	05:06:27
24756	24756.27	29	2015-05-20	05:43:59	2015-05-20	06:26:45
24756	24756.28	29	2015-05-20	06:37:02	2015-05-20	07:42:17
24756	24756.29	40	2015-05-20	07:59:38	2015-05-20	09:11:14
24756	24756.30	25	2015-05-20	09:22:31	2015-05-20	09:59:51
24756	24756.31	18	2015-05-20	10:34:55	2015-05-20	11:16:45
24756	24756.33	8	2015-05-20	14:30:29	2015-05-20	14:41:57
24756	24756.34	18	2015-05-20	15:02:49	2015-05-20	15:25:24
24756	24756.35	11	2015-05-27	11:06:45	2015-05-27	11:21:06
24756	24756.36	5	2015-05-27	12:55:09	2015-05-27	13:00:30
24756	24756.37	325	2015-05-27	16:47:15	2015-05-27	23:46:54
24756	24756.38	27	2015-05-28	00:00:32	2015-05-28	00:38:23
24756	24756.39	10	2015-05-30	09:10:01	2015-05-30	09:23:22
24756	24756.40	20	2015-05-30	23:10:24	2015-05-30	23:33:36

24756	24756.41	12	2015-06-04	12:15:57	2015-06-04	12:29:03
24765	24765.1	14	2015-06-23	22:51:50	2015-06-23	23:09:19
24765	24765.2	4	2015-06-24	00:22:47	2015-06-24	00:28:14
24765	24765.3	15	2015-06-29	03:00:21	2015-06-29	03:14:48
24765	24765.4	5	2015-06-30	02:49:49	2015-06-30	02:54:38
24767	24767.1	9	2015-06-03	00:17:54	2015-06-03	00:29:53
24767	24767.2	11	2015-06-08	04:38:18	2015-06-08	04:49:14
24767	24767.3	7	2015-07-12	07:52:04	2015-07-12	08:05:24
24767	24767.4	5	2015-07-14	20:41:57	2015-07-14	20:47:14

-

**Estimating spatial distribution, population size and trajectory of Nechako River white sturgeon
using a parametrically concise spatial capture-recapture model.**

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Comment [T1]:

The paper has been heavily overhauled following the comments of Carl and other reviewers. The paper is shorter and more focused on the case study. The changes are intended to provide a clearer narrative:

- (1) Integrating radio telemetry and PIT tagging data
- (2) Movement estimation for sparse recapture datasets
- (3) Integrating population dynamics to improve precision and realism of population size estimates.

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22 **Abstract**

23 Capture-recapture experiments are often used to assess rare or endangered populations of relatively low
24 numbers (e.g. less than 1000 individuals) where tag recapture data may be sparse. Spatial considerations
25 may also be important, for example it may not be defensible to assume zero immigration/emigration out
26 of a core population and tagging area. To address these issues we developed a parametrically concise
27 Bayesian, multi-state, Brownie capture-recapture model that can be fitted to spatial tagging data and radio
28 telemetry data. Using simulation we demonstrate that this approach provides robust estimates of
29 population size, trajectory and spatial population distribution. The spatial mark-recapture model was fitted
30 to the data for endangered Nechako River white sturgeon. Our spatial models provided a mean estimate of
31 545 Nechako River white sturgeon in 2015 (460 – 640, 90% probability interval) and predicted a
32 population decline to below 200 individuals in 25 years (16 - 37 years, 90% probability interval).

33

34 **Keywords**

35 Capture-recapture, multi-state, spatial, movement, tagging, *Acipenser transmontanus*, simulation
36 evaluation, Bayesian statistics.

Introduction

Nechako River white sturgeon (*Acipenser transmontanus*, Figure 1) is recognized as a distinct population based on spatial differences in habitat use (R. L. & L. 2000), genetic analysis (Smith et al. 2002; Schreier et al. 2012) and demographic differences (Korman and Walters 2001). Due to habitat changes at the only known spawning site (near Vanderhoof, Figure 1) the population has been undergoing chronic recruitment failure since 1967 leading to sustained population declines (McAdam et al. 2005). For this reason Nechako River white sturgeon has been classified as 'endangered' since 2003 and listed in the Species at Risk Act since 2006 (COSEWIC 2013).

Since the most recent population estimate of 571 fish (421-890, 95% confidence interval) in 1999 (R, L & L 2000) a greater quantity and quality of data have become available regarding the spatial extent of habitat use and movement among sub-regions of the Nechako watershed (Triton 2009). Updated estimates of current population numbers and rates of decline are critical for decision making. An improved understanding of spatial distribution and movement are also valuable and may help to define the geographic range of the population and inform spatial management approaches. The most important new data collection programs for Nechako River white sturgeon are mark-recapture experiments using internal Passive Inductive Transponder (PIT) and external anchor ('Floy') tags, in addition to an automated movement detection system using radio telemetry tags.

Mark-recapture analysis offers an established approach for estimating population size given these newly available tagging data. However in the case of Nechako River white sturgeon there are two principal problems in applying a conventional mark-recapture analysis. The first relates to spatial heterogeneity of the population and movement of individuals outside of a core tagging area. White sturgeon have been observed throughout the length of the Nechako River and in two major tributaries, the Stuart and Nautley rivers (which drains Fraser lake into the Nechako River). Sturgeon show a variety of movement patterns including local site fidelity (Nelson and McAdam 2012), repetitive seasonal exchange between habitats

Comment [TC2]: A principal criticism of reviews of the previous paper was that the introduction was not sufficiently comprehensive (presumably in its coverage of applicable mark-recapture analyses).

Perhaps Carl could highlight the key deficiencies and suggest appropriate references where possible.

It seems that the most important areas relate to:

- 1) multi-state spatial mark-recapture analyses
- 2) analysis of sparse recapture data
- 3) Integrated population dynamics-tagging models

Comment [T3]: Cory and Steve, perhaps you can comment further on

A) The use for absolute estimates of population size in the current management framework

B) the other potential benefits of understanding spatial population distribution and movement (ie why you did the radio telemetry).

(Parsley et al. 2008), and anadromous movements (Khodorevskaya et al. 2009). Although white sturgeon can occasionally undertake large-scale migrations, for example between the Columbia and Fraser Rivers (Welch et al. 2006), movement is generally over much smaller distances. In the Nechako River the majority of white sturgeon are found in a core tagging area (Area 2, Figure 2) and exhibit occasional movement to satellite areas (Areas 1, 3 and 4, Figure 2). It follows that the assumption of a single spatially homogeneous population is not reflected by tagging data and could potentially affect the reliability of population abundance estimates derived from a spatially-aggregated mark-recapture model.

The second important problem arising from the available mark-recapture data is that they are relatively sparse (typically less than 50 tags per year, Table 1) due to both small population abundance (less than 800 individuals) and low recapture probabilities (likely less than 5%). It follows that while a spatial mark-recapture analysis (e.g. Dupuis and Schwarz 2007) could provide a solution to estimating spatial heterogeneity and movement (addressing the first problem), it may be undesirable since additional spatial stratification of the recapture data would further reduce the number of recaptures per time-area strata and increase uncertainty in estimates of population size and trajectory.

In this research we developed a multi-state (spatial) capture-recapture model (e.g. Arnason 1973, Brownie et al. 1993 and Schwarz et al. 1993) based on the Brownie equations (1993). The model was developed in a Bayesian statistical framework to provide probabilistic estimates of population size and recapture probabilities. To improve precision of estimates of population size we integrated population dynamics (Maunder 1998; 2003) to constrain the model to credible population trajectories (i.e. chronic declines, McAdam et al. 2005). To improve the estimates of spatial distribution and movement between core and satellite areas we included likelihood functions for both PIT and radio telemetry tagging data (e.g. Powell et al. 2000). Furthermore we developed and simulated tested a parametrically concise gravity movement model (Carruthers et al. 2010; Taylor et al. 2011) to provide robust estimates of movement given sparse recapture data. We used simulation testing to validate the model and evaluate estimation bias. Finally we

applied the spatial models to the data for Nechako River white sturgeon to provide up-to-date estimates of population size and trajectory.

Materials and methods

MODEL STRUCTURE AND ASSUMPTIONS

A summary of the capture-recapture model variables, estimated parameters and data types can be found in Table 2.

Transition among states (movement among areas of individuals) was assumed to occur after sampling and before natural mortality. Survival rates s , recapture probabilities p , and return rates r , were calculated from instantaneous natural mortality rate M , and instantaneous sampling rate F . Parameterizing the model using instantaneous rates simplifies estimation since these parameters need only be constrained to be positive and it allows for straightforward calculation of survival and recapture probabilities over intermediate time intervals (e.g. eqn 1).

For an individual released in time period t , and area a , we assumed that in the initial time period, state transitions do not occur and sampling and natural mortality rates are half that of subsequent time steps. After the initial release time period, the probability of an individual surviving and being in state \bar{a} , at time \bar{t} , was calculated by multiplying survival to the previous time step (over k areas) by the state transition (movement) matrix θ , subject to sampling and natural mortality in the current time step:

$$(1) \quad s_{t,a,\bar{t},\bar{a}} = \begin{cases} \exp(-(M + F_{\bar{t},\bar{a}})/2) & \bar{t} = t \\ \sum_k [\theta_{k,\bar{a}} \cdot s_{t,a,\bar{t}-1,k} \cdot \exp(-F_{\bar{t},\bar{a}} - M)] & \bar{t} > t \end{cases}$$

112 Note that in this context, the term survival refers to the probability of a tagged individual being both alive
 113 and not recaptured. Similarly to Dupuis and Schwarz (2007) when individuals are recaptured they are re-
 114 released and re-enter the model as a new release event.

115
 116 Similarly to sampling rates, recapture probabilities p , were calculated from half the sampling rate in the
 117 initial release year and was given by:

118

$$119 \quad (2) \quad p_{t,\bar{t},\bar{a}} = \begin{cases} 1 - \exp(-F_{\bar{t},\bar{a}}/2) & \bar{t} = t \\ 1 - \exp(-F_{\bar{t},\bar{a}}) & \bar{t} > t \end{cases}$$

120

121 Return rates r (the probability a tag released at time t , in area a , is recaptured in time \bar{t} , area \bar{a}) were
 122 calculated as the product of survival and probability of recapture:

123

$$124 \quad (3) \quad r_{t,a,\bar{t},\bar{a}} = s_{t,a,\bar{t},\bar{a}} \cdot p_{t,\bar{t},\bar{a}}$$

125

126 The return rates were used to calculate the likelihood of the observed recapture data using a multinomial
 127 likelihood function (Table 2, see section ‘Estimation’ below)

128

129 By integrating a simple population dynamics model, predicted population trajectories were constrained to
 130 continual declines according to the natural mortality rate M , that was assigned a prior probability
 131 distribution and updated by the capture-recapture model. Total population numbers in the first time-step
 132 (N_0) are estimated and distributed into spatial areas according to the vector d :

133

$$134 \quad (4) \quad N_{1,a} = d_a N_0$$

135

136 where d is the asymptotic population distribution given the movement matrix θ , satisfying the condition
 137 $d=\theta d$. The vector d can be calculated analytically; it is the positive eigenvector of the movement
 138 probability matrix θ , corresponding to the first eigenvalue. Alternatively d can be approximated
 139 numerically by repeatedly multiplying an initial distribution vector d (sums to 1) by θ until d stabilizes.

140
 141 Population numbers in any future time step is given by multiplying the previous population numbers by
 142 the movement matrix θ , accounting for natural mortality rate:

143
 144 (5)
$$N_{t+1,a} = \sum_k \theta_{k,a} N_{t,k} \exp(-M)$$

145
 146 Total predicted numbers of individuals caught (both recaptures and new captures) \hat{C} in any time-area
 147 strata are given by:

148
 149 (6)
$$\hat{C}_{t,a} = N_{t,a} (1 - \exp(-F_{t,a}))$$

150
 151 which can then be compared to observed individuals caught (C) via a lognormal likelihood function
 152 (Table 1, see section ‘Estimation’ below). Additional radio telemetry data are available the Nechako
 153 River that provide observations of movement transitions among areas (Y). To allow additional radio
 154 telemetry data to inform movement we compared these to predicted movement transitions θ , using a
 155 multinomial likelihood function (Table 2).

156 157 MODELLING MOVEMENT

158 Two approaches to parameterizing movement were investigated: (1) a fully-specified Markov movement
 159 matrix and (2) a more parametrically concise gravity model (Carruthers 2010; Taylor et al. 2011). In both

160 movement models, the probability of an individual moving from area a to an area k , $\theta_{a,k}$ is calculated by a
 161 logit function to constrain rows to sum to 1:

162

$$163 \quad (7) \quad \theta_{a,k} = \exp(G_{a,k}) / \sum_k \exp(G_{a,k})$$

164

165 The first term of each row is fixed to zero and not estimated ($G_{r,l}=0$) and all other G terms are estimated.

166 It follows that the fully specified Markov matrix requires the estimation of $n_a (n_a-1)$ movement
 167 parameters, where n_a is the number of areas (states).

168

169 The alternative gravity model approach assumes that movement from area a to area k is proportional to a
 170 gravity weight for area k , and that the probability of remaining in the same area, is proportional to that
 171 gravity (with slope, viscosity, v). In the case of the gravity model, the G terms are not estimated
 172 individually but calculated by:

173

$$174 \quad (8) \quad G_{a,k} = \begin{cases} g_k & a \neq k \\ g_k + v & a = k \end{cases}$$

175

176 Although the gravity model is more constrained, it is much more parametrically concise and requires the
 177 estimation of just n_a parameters. These are the n_a-1 gravity terms g , (similarly to the fully described
 178 movement model above, g_l is fixed to zero) and a single viscosity parameter v . It follows that in the case
 179 of a 10 areas, the gravity model requires the estimation of just 10 movement parameters rather than 90 for
 180 the fully specified Markov model.

181

182 ASSUMPTIONS

183 In order to interpret survival rate in terms of natural mortality rate and sampling rate, emigration and
 184 immigration outside of the modelled areas was assumed to be zero. We assumed that tag shedding rates

185 were zero, tag reporting rates were 100% and tag detection rate was 100% for both the conventional tag
 186 recaptures and radio tags. Additionally we also assumed that tagged and non-tagged individuals had the
 187 same natural mortality rate, movement rate and probability of recapture as tagged individuals.

Comment [T4]: Perhaps a comment from Steve or Cory on why these may be reasonable (or not!) assumptions

188

189 ESTIMATION

190 There were four objective function components associated with the PIT tagging recaptures R , PIT tags
 191 that were released but not recaptured U , movement observations among areas recorded by telemetry Y ,
 192 and observed total catches of individuals C (both tagged and untagged fish).

193

194 Observed PIT tags R recaptured in time period \bar{t} and area \bar{a} , originating from a release in time period t ,
 195 and area a , were assumed to be distributed multinomially. The objective function component associated
 196 with tag recaptures O_R was the negative log-likelihood of a recapture R , given the model predicted return
 197 rate r :

198

$$199 \quad (9) \quad O_R = -\sum_t \sum_a \sum_{\bar{t}} \sum_{\bar{a}} R_{t,a,\bar{t},\bar{a}} \cdot \log(r_{t,a,\bar{t},\bar{a}})$$

200

201 This was extended to unrecaptured tags U , originating from a release in time period t , and area a :

202

$$203 \quad (10) \quad O_U = -\sum_t \sum_a U_{t,a} \cdot \log(1 - \sum_{\bar{t}} \sum_{\bar{a}} r_{t,a,\bar{t},\bar{a}})$$

204

205 Similarly, radio telemetry observations Y , of a fish leaving an area a and entering an area k in the
 206 subsequent time period, were also assumed to follow a multinomial distribution determined by the
 207 estimated movement matrix θ :

208

$$209 \quad (11) \quad O_Y = -\sum_a \sum_k Y_{a,k} \cdot \log(\theta_{a,k})$$

210
 211 Observed total captures (recaptures of both tagged and untagged fish) C , were assumed to be log-
 212 normally distributed and the associated objective function component O_C , was the negative log likelihood:
 213

$$214 \quad (12) \quad O_C = \sum_t \sum_a \frac{\log(\sigma_C) + (\log(\hat{c}_{t,a}) - \log(c_{t,a}))^2}{2 \cdot \sigma_C^2}$$

215
 216 Where σ_C is the log-normal standard deviation for catch observations.
 217

218 Non-informative (uniform on log) priors for various model parameters were prescribed including, initial
 219 population numbers N_0 , movement parameters G , g , viscosity v and sampling rate F (Table 1) while an
 220 informative log-normal prior was assumed for natural mortality rate:
 221

$$222 \quad (13) \quad O_M = \frac{\log(\sigma_M) + (\log(\bar{M}) - \log(\bar{M}))^2}{2 \cdot \sigma_M^2}$$

223
 224 where \bar{M} and σ_M are the mean and standard deviation of the lognormal prior distribution, respectively.
 225

226 The global objective function to be minimized was the summation of the objective components:
 227

$$228 \quad (14) \quad O_G = O_R + O_U + O_V + O_C + O_M$$

229
 230 The model was implemented in AD Model Builder (Fournier et al. 2012) allowing for the rapid and
 231 robust estimation of posterior modes for model parameters using the AUTODIFF routines. Using ADMB,
 232 probabilistic estimates of model parameters and variables were obtained using Markov Chain Monte
 233 Carlo simulation via the Metropolis-Hastings algorithm. Simulation evaluation was carried out using the

234 R statistical environment (v3.2.3 64bit, R Development Core Team 2016). The R package ‘coda’ was
235 used to evaluate convergence using trace plots of the MCMC chains, Gelman and Rubin (1992) and
236 Geweke (1992) diagnostics. For all Bayesian analyses applied here, convergence could not be rejected
237 given 500,000 MCMC samples with a ‘burn-in’ of 50,000 iterations.

238

239 The spatial models and code for undertaking the analyses of this paper can be accessed at
240 <https://github.com/tcarruth/spatialCR>.

241

242 SIMULATION STUDY: TESTING A PARAMETRICALLY CONCISE MOVEMENT MODEL

243 Parametrically concise movement models have been applied previously in the estimation of population
244 size for a number of tuna and billfish species (Carruthers et al. 2010; Taylor et al. 2011). However those
245 studies did not thoroughly investigate the circumstances under which the simpler gravity models reliably
246 evaluate population size.

247

248 A ‘crossed’ simulation test was carried out in which gravity and Markov movement processes were
249 simulated, to which both gravity and fully specified Markov movement models were applied. The purpose
250 of this simulation was to better describe the interaction of the movement assumptions and identify
251 possible estimation biases.

252

253 The simulations were configured to be as similar as possible to the Nechako River white sturgeon case
254 study (below): capture-recapture data were available for 16 time-steps (years), population numbers were
255 simulated to start at 1000 individuals, average annual sampling intensity was 5% of the population and
256 natural mortality rate was assumed to be 0.04yr^{-1} . When not varied systematically in the five sensitivity
257 analyses above, viscosity (v , eqn 8) was set to 4 (~95% probability of staying in a given area between
258 time steps), the total number of telemetry observations was 500 (Table 1) and movement probabilities
259 (parameters G and g eqn 8) were sampled from a normal distribution with a mean of zero and CV of 1

(areas could contain as little as 1% of the total population). We chose current population size as the variable of interest with which to examine biases.

CASE STUDY: NECHAKO RIVER WHITE STURGEON

Two sources of tagging data are available for Nechako River white sturgeon that differ in the information they provide: (1) conventional tags that were either internal Passive Inductive Transponder (PIT) type or external anchor ('Floy') tags and (2) radio telemetry tags. The PIT and anchor tags are the primary source of data to inform the spatial mark-recapture models of this paper. A subset of the fish are also tagged with radio telemetry tags that are subsequently detected by a mixture of mobile and fixed radio detection systems providing information about exchange among areas that is independent of the capture-based sampling activities. In this analysis we use data beginning in 2001 for which around 40-50 anchor tags were released per year and there are a total of 500 telemetry observations (Table 1). To represent the relatively precise reporting of PIT recaptures in the Nechako River, total catch observation error σ_C was assumed to be low (a coefficient of variation of 5%).

Four discrete spatial areas were defined for Nechako River white sturgeon that relate to habitat and life-history (Figure 2). Area 1 ('Lower Nechako and Stuart') is a low population density area for which occasional movements have been detected. It is defined by the confluence of the Nechako and Stuart Rivers; all areas downstream in the Nechako River and upstream in the Stuart River, including Stuart Lake are considered to be Area 1. Area 2 ('Lower Core Area') is of moderate population density and thought to be an important feeding area; it is comparatively small and is the 17km stretch of the Nechako River immediately upstream of the Stuart River confluence. Area 3 ('Upper Core Area') is a high population density area that is the primary location for overwintering, staging and spawning. Area 3 is defined as the 31 km stretch of the Nechako River immediately upstream of Area 2. Finally, Area 4 ('Upper Nechako and Fraser Lake') is all river and lake areas upstream of Area 3 including Fraser Lake. Similarly to Area 1, this is a low population density area associated with occasional distant movements.

286
287 A default prior for natural mortality rate was specified with mean 0.04yr^{-1} and a coefficient of variation
288 of 20% (an intermediate level given the range of 0.025-0.05 that was considered credible for Fraser River
289 white sturgeon; Whitlock and McAllister 2012).

290

291 **Results**

292 SIMULATION STUDY: TESTING A PARAMETRICALLY CONCISE MOVEMENT MODEL

293 The 'crossed' simulation evaluation of the gravity model assumptions indicates that gravity models and
294 Markov models performed similarly regardless of whether gravity dynamics or full specified Markov
295 movement dynamics were simulated (Figure 3). In all cases, estimates of current population decline were
296 slightly negatively biased (mean estimates between -4% and -7%) with 90% of estimates falling in the
297 range of -50% to 40% (Figure 3). Conversely, estimates of current population size were slightly positively
298 biased (mean estimates between 2% and 4%) and unlikely to be strongly biased with 90% of estimates
299 falling between -10% and 20%.

300

301 CASE STUDY: NECHAKO RIVER WHITE STURGEON

302 Consistent with the simulation results above, when applied to the PIT and telemetry tagging data for
303 Nechako River white sturgeon, gravity and Markov movement models provided very similar estimates of
304 population size and trajectory. Both models estimate current population size of 545 individuals with a
305 90% probability interval of between 460 and 640 individuals (Figures 4 and 5).

306

307 The gravity and Markov models also provided the same posterior estimates of natural mortality rate that
308 showed very little update over the prior distribution (posterior mean of 0.042 and CV of 0.18 compared
309 with a prior mean 0.04 and CV of 0.2) (Figures 5 and 6). Given these estimates the Nechako River white
310 sturgeon population is predicted to decline below 200 individuals in 25 year (with a 90% probability
311 interval of 16 to 37 years).

312
313 The data do not update a much lower prior for natural mortality rate (a posterior mean of 0.022 given a
314 prior with mean of 0.02) but do substantially update a higher prior for natural mortality rate (a posterior
315 mean of 0.065 given a prior mean of 0.08) (Figure 6, panels b and c) . A vague prior for natural mortality
316 was also informed more strongly by the data (posterior with mean 0.041 with a CV 0.031 given a prior
317 with mean 0.04 and CV of 0.5) (Figure 6, panel d). This result suggests the data are broadly consistent
318 with natural mortality rates prescribed in the default model runs or a lower prior value, in which case the
319 population would be declining slower than predicted given the default prior.

320
321 While gravity and Markov models may provide similar estimates of current population size and trajectory
322 they can offer quite different predictions of movement probabilities and the predicted spatial distribution
323 of the population (Table 3). For example, the gravity model predicts that 52% and 7% of individuals in
324 the Lower Core area (area 2) will move to the Upper Core area (area 3) between years, respectively. For
325 the Markov model these estimates are 67% and 0%, respectively. The Markov model estimates that
326 movements from the Lower Nechako (Area 1) to the Upper Nechako (area 4) are infrequent at an annual
327 rate of 5%. The gravity model on the other hand estimate a much higher movement rate of 17%. While
328 these differences reflect the constrained nature of the gravity model, the asymptotic spatial distributions
329 predicted by these differing movement matrices are very similar (Table 3).

330

331 **Discussion**

332 We developed a Bayesian multi-state Brownie capture-recapture model that incorporates both
333 conventional tag and telemetry data. The model was used to test parametrically concise gravity models for
334 estimating state (movement) transitions for datasets with sparse recapture data. We applied the model to
335 the data for Nechako River white sturgeon to estimate current abundance and trajectory for this critically
336 endangered population. The gravity and Markov models provided almost identical estimates. Both
337 provided a mean population size estimate of 545 individuals in 2015. This estimate is considerably

Comment [TC5]: This is very much draft at this point. It would be great to pick your brain Carl, over the important references and discussion points relative to similar work elsewhere.

338 higher than the previous estimate of 571 fish (R. L. & L. 2000) given that the previous estimate was for
339 the population 13 years ago (333 fish in 2015 given a natural mortality rate of 0.04). Whitlock and
340 McAllister (2012) also obtained larger estimates of population size than a spatially aggregated model that
341 was attributed to correctly accounting for spatial heterogeneity. In our analyses, population trajectories
342 were estimated much less precisely: between 16 and 37 years for the population to drop below 200
343 individuals (90% probability interval).

344

345 < Steve and Cory, discussion points on the upshot of the model estimates of numbers and trajectory ?>

346

347 Simulation evaluation reveals that parametrically concise gravity models can provide similarly robust
348 estimates of population status and spatial distribution as more complex fully specified movement models.
349 When applied to the data for Nechako River white sturgeon, the less constrained Markov model could
350 provide very different estimates of movement probabilities between certain areas. However both gravity
351 and Markov models provided very similar estimates of the asymptotic spatial distribution of the
352 population and very similar estimates of population size and trajectory. These results indicate that the
353 central problem addressed by spatial models pertains to the approximation of spatial heterogeneity in the
354 population, and that this can be suitably addressed by much simpler gravity models. Markov movement
355 models can provide a much more detailed account of the area-by-area movements that underpin that
356 heterogeneity but this is not critical to providing reliable estimates of population size and trajectory. It
357 follows that if data are sparse the more tractable gravity model could be an option worth pursuing.
358 Although not tested here, an even simpler approach that estimates a constant fraction of the population in
359 each area may also be an option, although this would save just one additional parameter over the gravity
360 model (the viscosity parameter ν).

361

362 There are however, circumstances in which it might be advisable to apply the Markov movement model.
363 The issue relates to the gravity equations that impose an assumption that the probability of individuals

staying in an area is proportional to the gravity weight of that area. When estimating movement this requires careful definition of the discrete areas. Suppose for example that we had further split into two areas, the upper core area of the Nechako River case study where most of the tags are released and recaptured. In reality, both of these areas constitute a large fraction of the population (high gravity weight) whilst having relative low probability of individuals remaining in these areas (there is high exchange among different parts of the upper core area) which violates the central assumption of the gravity model. In this example applying the gravity instead of the fully specified movement model could lead to erroneous management advice. For example false predictions of high retention in each of these areas might underestimate the impact of habitat degradation in the adjacent area.

A simple population dynamics model was integrated into the capture-recapture estimator to greatly constrain the time-series of estimated population size. Integrated capture-recapture models are common in the fisheries population modelling literature (Hampton & Fournier 2001, Adam & Sibert 2002) and amongst the most complex approaches have estimated seasonal movements for multiple populations using a combination of conventional tags, electronic tags and otolith microchemistry data (Taylor et al. 2011). Very simple spatial models (Carruthers et al. 2010) have been used to demonstrate that tagging data are not required in order to reliably estimate the parameters of the simple gravity model, allowing spatial distribution of the population and movement to be estimated from only regional abundance trend information (e.g. transect surveys).

One of the core advantages of developing a custom multi-state model in the AD Model builder software (Fournier et al. 2012) using AutoDiff libraries, was the improvement in model speed over existing capture-recapture software such as MARK (White and Burnham 1999). With 16 years and 4 states, the models obtained maximum posterior density estimates in less than 10 seconds on a performance laptop and could generate over 500,000 MCMC samples in under 5 minutes. This robust and rapid estimation

performance suggests that the model could be applied to more complex data over many more years and states.

It should be noted that model predictions of population trajectory were highly sensitive to the prior specification of natural mortality rate. Mean estimates of the time until the population declines below 200 individuals were 56 years and 12 years for model with natural mortality rate priors of 0.02yr^{-1} and 0.08yr^{-1} , respectively. This suggests that the tagging data may be informative regarding absolute population size but weakly informative with regard to population trajectory which is also confirmed by the modest posterior update in natural mortality rate given alternative priors. This effect is due to the relatively short time-series of tagging data and the longevity of white sturgeon. While natural mortality rate is likely to be better characterized by tagging data as the programme continues, this may be slow relative to the possible rate of decline in population size.

To some extent the Nechako River white sturgeon case study is unusual and adheres particularly well to the common assumptions of capture-recapture analyses. Detection rates and reporting rates are likely to be 100%, and shedding and release mortality rates, very close to zero. It is also safe to assume negligible emigration and immigration outside of the four areas that were modelled, a condition that may be not appropriate for many wild animal populations.

< Wrap up conclusions >

Acknowledgements

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414

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498 reduction analysis for lower Fraser River white sturgeon (*Acipenser transmontanus*). Can. J. Fish.
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500 **Tables**

501 Table 1. Summary of Passive Inductive Transponder (PIT), anchor tagging and telemetry data for the
 502 Nechako River case study (see Figure 2 for area definitions).

PIT tags and anchor tags

Total fish caught (initial captures + recaptures)

Year	Area			
	1	2	3	4
2001	3	0	53	0
2002	4	5	0	0
2003	0	0	0	0
2004	2	0	7	0
2005	0	1	46	0
2006	0	0	40	0
2007	2	0	40	0
2008	0	0	70	0
2009	0	0	84	0
2010	0	0	57	0
2011	0	0	64	0
2012	0	0	35	0
2013	0	0	22	0
2014	13	0	65	0
2015	1	0	37	1
Total	25	6	620	1

N = 652

Radio telemetry

Fish observed moving from an area to an area

Area From	To			
	1	2	3	4
1	23	10	26	1
2	3	10	28	0
3	44	22	289	21
4	1	1	15	6

N = 500

503

504 Table 2. Capture-recapture model parameters, variables and data types including prior probability
505 distributions and likelihood functions. Priors and likelihood functions are given abbreviated distribution
506 names where LN=lognormal, U=uniform and MN=multinomial. Lognormal mean and standard deviation
507 variation are abbreviated to μ and σ , respectively.

Model variable	Symbol		
Population numbers	N		
Predicted catches	\hat{C}		
Survival rate	s		
Return rate	r		
Probability of recapture	p		
State transition (movement) probability	θ		
Estimated parameter		Prior distribution	Specific model
Natural mortality rate	M	$M \sim \text{LN}(\mu=0.04, \sigma_m=0.2)$	
Initial population numbers	N_0	$N_0 \sim \text{U}(0, \infty)$	
Sampling rate	F	$\log(F) \sim \text{U}(-10, 0.4)$	
Logit space transition probability	G	$\log(G) \sim \text{U}(-6, 6)$	Markov
Gravity	g	$\log(g) \sim \text{U}(-6, 6)$	Gravity
Viscosity	v	$\log(v) \sim \text{U}(-6, 6)$	Gravity
Data		Likelihood function	
Observed catches	C	$C \sim \text{LN}(\mu=\hat{C}, \sigma_c=0.05)$	
Observed recaptures	R	$R \sim \text{MN}(r)$	
Tags not recaptured	U	$U \sim \text{MN}(1-\Sigma r)$	
Telemetry movements	Y	$Y \sim \text{MN}(\theta)$	

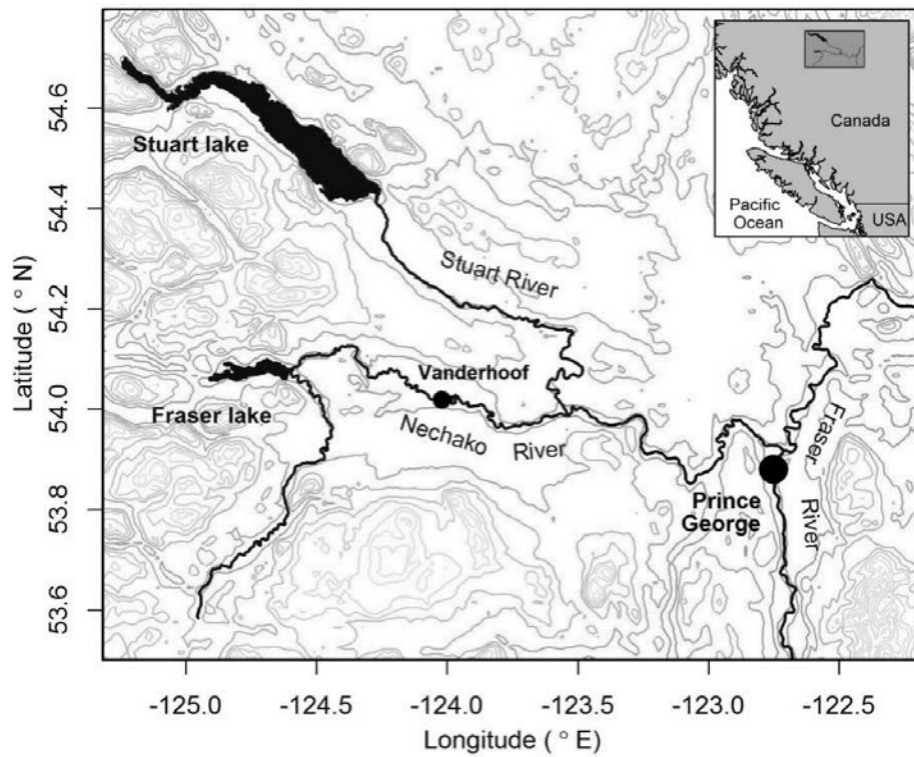
510 Table 3. Movement probability matrices estimated by the gravity and Markov movement. All numbers are
511 maximum posterior density estimates and are expressed as percentages. The 4 by 4 area movement
512 matrices provide the probability of moving from an area (by row) to an area (by column). The predicted
513 population distributions are the spatial distribution of the population given the estimated movement
514 matrices.

(a) Gravity movement model		Moving to (%)			
Moving from		Area 1	Area 2	Area 3	Area 4
Area 1: Lower Nechako and Stuart		36.66	9.12	47.99	6.24
Area 2: Lower Core Area		16.25	24.53	52.40	6.81
Area 3: Upper Core Area		10.02	6.14	79.63	4.20
Area 4: Upper Nechako and Fraser Lake		17.04	10.44	54.94	17.59
Asymptotic population distribution		14.89	8.36	71.30	5.45

(b) Markov movement model		Moving to (%)			
Moving from		Area 1	Area 2	Area 3	Area 4
Area 1: Lower Nechako and Stuart		40.45	16.25	41.71	1.59
Area 2: Lower Core Area		7.92	24.71	67.35	0.02
Area 3: Upper Core Area		11.04	5.32	78.61	5.03
Area 4: Upper Nechako and Fraser Lake		4.66	4.38	65.00	25.96
Asymptotic population distribution		14.79	8.54	71.49	5.18

515

516 **Figures**



517

518 Figure 1. The location and topology of the Nechako River basin.

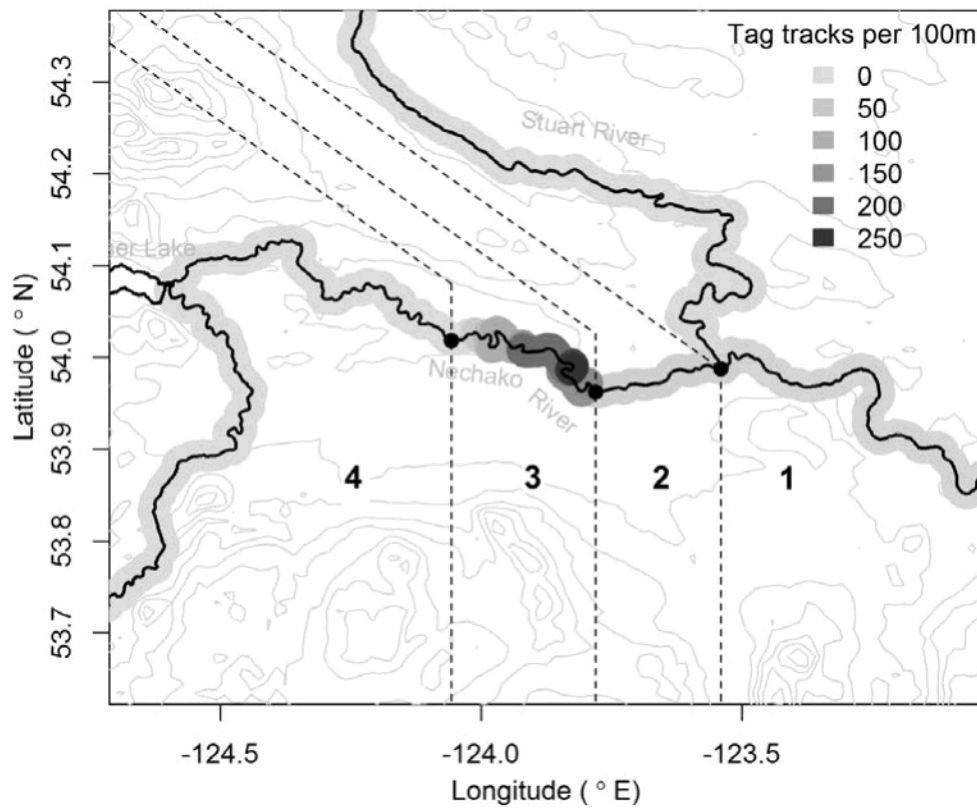
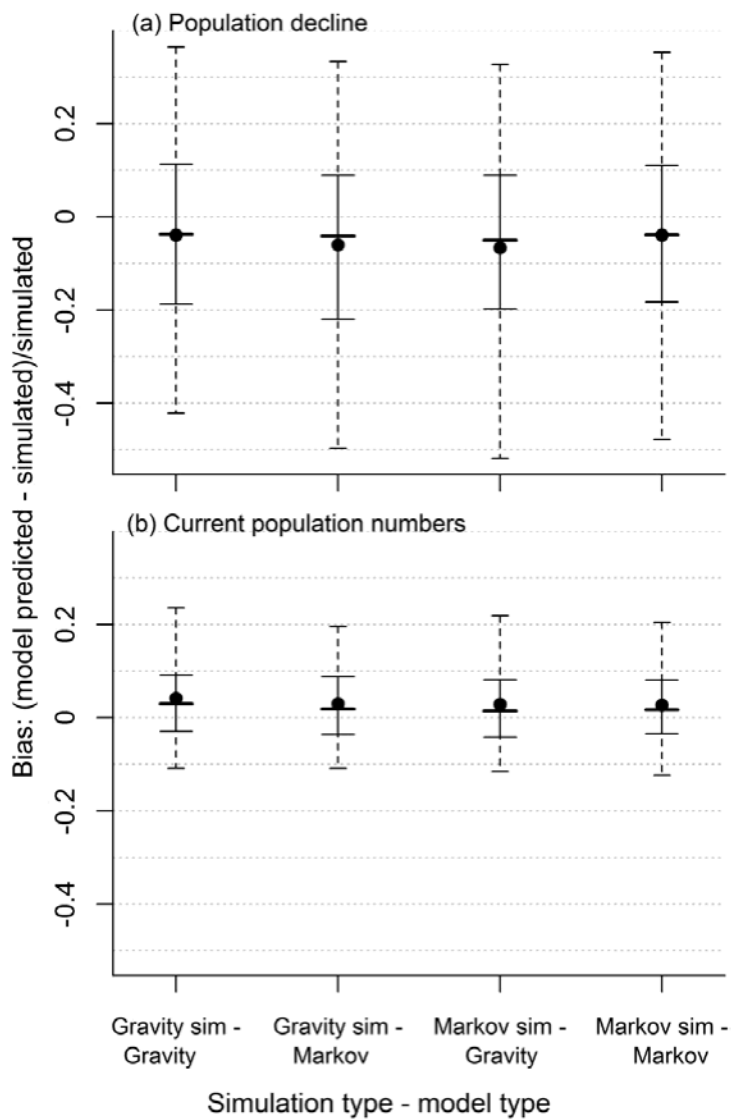
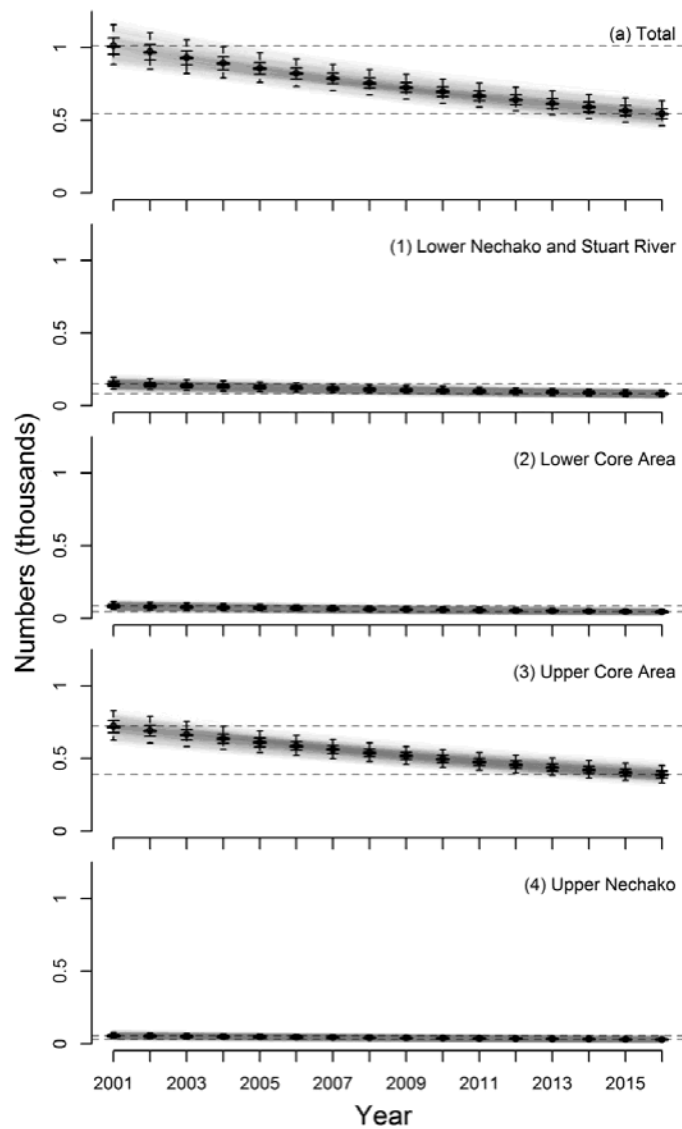


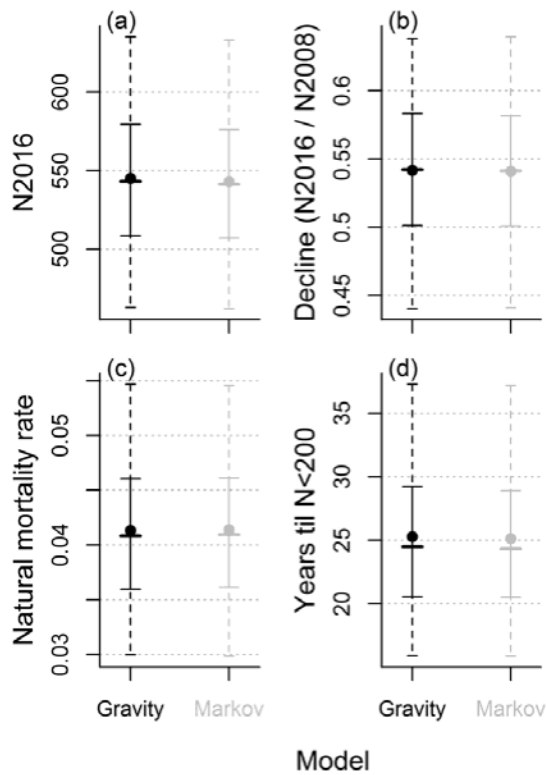
Figure 2. Tag-track density and area definitions for the Nechako River white sturgeon case study. Track density is represented by the shading where red indicates river sections that were most often traversed when joining tag release location to tag capture location. Radio telemetry movement data were collected at the boundaries of the four areas (where the dashed lines cross the river)



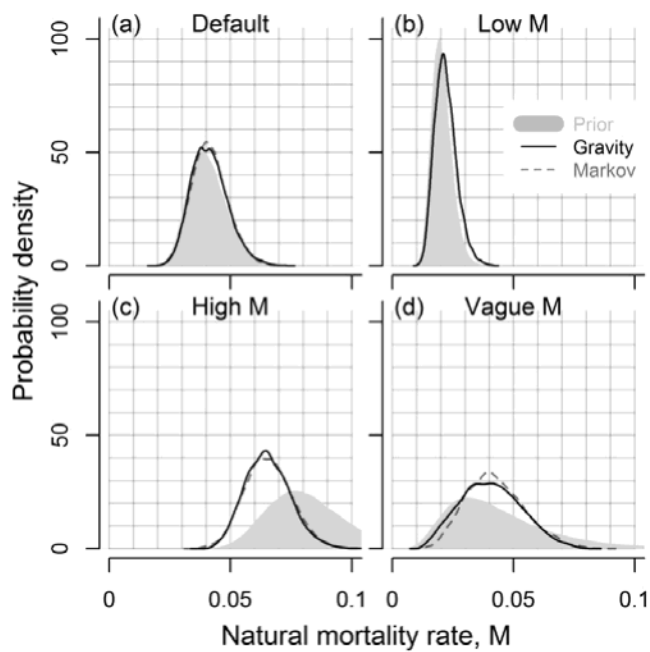
524
 525 Figure 3. The estimation bias of the gravity model and fully described Markov movement model applied
 526 to populations simulated with gravity (Gravity sim) and fully described Markov movement models
 527 (Markov sim). Panel a illustrates bias in the estimation of population decline (numbers at end of time
 528 period / numbers at start of time period). Panel b illustrates bias in the estimation of current population
 529 size. Each bar represents 500 simulations / mean posterior estimates.



530
 531 Figure 4. The posterior predicted total numbers of Nechako River white sturgeon (panel a) and numbers
 532 by area (panels b-e) predicted by the gravity movement model. Plotted points represent mean posterior
 533 estimates. Bold horizontal ticks represent median posterior estimates. Solid vertical bars are the 50%
 534 probability intervals. Dashed vertical bars are the 90% probability intervals. Horizontal dashed lines
 535 represent mean estimates at the start and end of the time series.



536
 537 Figure 5. Posterior predictive distributions for model estimates for the Gravity and Markov models. N2008
 538 and N2016 refer to estimated stock numbers in 2008 and 2016, respectively. Plotted points represent
 539 mean estimates. Bold horizontal ticks represent median estimates. Vertical solid lines represent the
 540 interquartile range, dashed vertical lines represent the 90% probability interval.



541
 542 Figure 6. Posterior update in natural mortality rate from various prior distributions. Panel a shows the
 543 posterior probability distribution of the gravity and Markov models given the default prior distribution for
 544 natural mortality rate with a mean of 0.04yr^{-1} and coefficient of variation 20%. Panels b and c are priors
 545 with means of half and double (0.02yr^{-1} and 0.08yr^{-1}) the default rate, respectively. Panel d represents a
 546 prior that is less precise than the default value (coefficient of variation = 50%).

1
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36
37 **Summary**
38
39 Habitat loss is widely recognized as a substantial contributor to global declines in
40 sturgeon populations yet habitat remediation has been limited for this highly
41 endangered group of fish. Of 19 remediation projects identified more than half
42 show limited long term success. In support of future sturgeon restoration efforts,
43 this review examines the needs and uncertainties regarding spawning habitat
44 remediation, including associated biological and physical monitoring. Four case
45 studies are presented that examine four distinct remediation contexts (mitigation,
46 rejuvenation, re-creation, repatriation) and three bio-spatial scales (whole river,
47 spawning reach, spawning location) under which remediation has been attempted.
48 Material presented in this review will support more timely and effective
49 remediation, and better align sturgeon research and monitoring approaches. The
50 limited number of sturgeon spawning habitat remediation projects to date attests

51 to the importance of learning from existing projects and cross species comparisons
52 to maximize the effectiveness of future sturgeon restoration efforts.

53

54 **Introduction**

55 Overfishing and habitat loss are the predominant causes of sturgeon declines
56 worldwide (Rosenthal and Pourkazemi 2006). Within the broad category of habitat
57 loss a wide array of anthropogenic changes have been identified, including river
58 regulation for navigation, flood prevention and power generation, and pollution
59 from industrial activities (e.g., Luk'yanenko et al. 1999, Secor et al. 2002, Gessner
60 and Jarić 2014). River regulation has had particularly strong effects on sturgeon due
61 to impacts including habitat fragmentation (Jager et al. 2001), blocked migration,
62 and both direct (e.g., daily and seasonal flow modification) and indirect (e.g.,
63 temperature, nutrient levels, hydraulic conditions, substrate) effects of flow
64 regulation (Petts 1984, Petts et al. 1989, Ward and Stanford 1989). The vulnerability
65 of this ancient group of fishes to river regulation is further increased by their
66 restriction to large rivers of the northern hemisphere, most of which are regulated
67 or highly modified (Dynesius and Nilsson 1994).

68 Human disruption of natural hydro-geomorphological processes that create and
69 maintain riverine habitats, as well as outright habitat destruction, has progressed to
70 the point that remediation is necessary in order to sustain habitat conditions for
71 natural reproduction of many sturgeon species. Despite widespread loss and
72 alteration of sturgeon habitats worldwide habitat restoration has been limited for
73 this highly endangered group of fish. Three key factors may underlie the limited
74 remediation to date. First, the ultimate causes of riverine habitat alterations that
75 affect sturgeon (i.e. construction of shipping channels or large dams) are often
76 considered irreversible impacts (Petts 1989, Petts et al. 1989, Ligon et al. 1995).
77 Second, biological uncertainty continues to limit the identification of effective
78 remediation measures. Thirdly, greater consideration of geomorphological effects is
79 needed to ensure the effectiveness of remediation works. The dire conservation
80 status of many sturgeon (Pikitch et al. 2005) emphasizes the need for timely action.
81 A few notable examples provide confidence that physical habitat remediation can
82 be successful (Dumont et al. 2011), as does substantial experience with other fish
83 species where habitat restoration research is further developed (e.g., salmonids;
84 Wheaton et al. 2004).

85 Understanding current habitat limitations is an important requirement for effective
86 habitat remediation (Rosenfeld and Hatfield 2006), and for most sturgeon detailed
87 knowledge of their habitat requirements limits remediation. General habitat use
88 has been described for many species (Bemis and Kynard 1997, Fox et al. 2002,
89 Fisheries and Oceans Canada 2014) Chang et al. 1995, Hatin et al. 2006, Clugston et
90 al. 1995, Fox et al. 2002, Jager et al 2002), however, few studies have specifically

identified limiting habitats (e.g. McAdam 2015) Restoration needs may vary substantially depending on the causes of population declines. In some cases remediation may be required throughout modified river corridors. In some cases site specific remediation may be sufficient, for example the remediation of spawning and early rearing habitats.. While a broad spectrum of remediation needs is discussed we focus on remediation of spawning and early rearing habitat. This focus stems from the consensus that early life history survival is critical to recruitment and the identified links between recruitment failure and impacts to spawning habitat (McAdam et al. 2005, Paragamian et al. 2009, McAdam 2012) (Gessner et al. 2009, McAdam 2011, Hastings et al. 2013, McAdam 2015). Additionally most remediation to date has focussed on spawning habitat. Conservation fish culture has also been more widely employed to mitigate immediate extirpation risks for many populations, and if carried out with necessary precaution can provide an interim compensation for low recruitment (Chebanov et al. 2002, Ireland et al. 2002, Secor et al. 2002). However, conservation fish culture is not discussed in this review based on the principle that natural reproduction must be the ultimate goal of recovery efforts.

Our investigation of sturgeon restoration needs identified the importance of contextual (e.g., creation of novel habitats versus improvements to existing habitat; Table 1) and biophysical (Table 2) factors that influence the scale of restoration. For example, repatriation to formerly occupied rivers, potentially including the need for fish passage (e.g. European sturgeon) presents substantially greater challenges due to the need for *de novo* habitat creation and the need to address multiple spatial scales and life stages. For most species the presence of continued biological uncertainty means that a “build it and they will come” approach entails substantial risk. The large scale of potential recovery projects also means that economic risks may be substantial. Our objective in this review is to decrease such risks and support more timely and effective restoration based on an overview of the current literature and the examination of four case studies. Although spawning habitat restoration is the focus of this review, other forms of habitat restoration (e.g. fish passage or flow regimes) are also discussed. In order to maximize benefits and learn from current restoration projects this review also promotes cross species comparisons, which are arguably too infrequent in sturgeon restoration.

Approaches to spawning habitat remediation

We identified four remediation contexts and three bio-spatial scales (Tables 1 and 2) that provide a structured way to consider the expected complexity of remediation (Table 3). The need to address remediation at the watershed scale is a function of the large river habitats occupied by sturgeon, and the long distance migrations shown by some species. We also note that our focus on spawning habitat restoration reflects the current suite of remediation efforts. This skew

131 towards smaller remediation focussed on spawning habitat likely occurs because
132 most current remediation works address pre-existing projects (e.g. dams) that did
133 not address sturgeon migratory needs when they were constructed. Our focus on
134 spawning habitat restoration therefore reflects current projects, and should not be
135 interpreted to indicate that larger scale remediation is not required. The need to
136 consider a large range of spatial scales is also driven by continued uncertainty
137 regarding mechanisms of population regulation, and remediation approaches will
138 be refined as biological knowledge improves. For example, assumptions regarding
139 the spatial scale of larval drift requirements (e.g., Gessner et al. 2009, McAdam
140 2011, Wildhaber et al. 2011) have strong effects on the spatial scale of
141 remediation¹. Our discussion of the biological requirements associated with
142 sturgeon restoration needs progresses from larger to small spatial scales.

143

144 Many sturgeon undergo large scale migrations (e.g. 1,000s of km for CS, ref), and
145 lost connectivity is a widely recognized impact of river regulation. The high
146 energetic cost of long distance upstream migrations implies that the biological
147 benefits of such migrations are substantial. Migrations to specific spawning reaches
148 still occurs for some species in certain rivers (Duong et al. 2011, Fisheries and
149 Oceans Canada 2014) and maintaining current levels of riverine connectivity may be
150 critical for those populations. While spawning downstream of migratory barriers is
151 widely observed, such locations may not provide the biological benefits associated
152 with upstream spawning migrations (see below), and substantial. For example, lost
153 migratory access may concentrate spawning in tailrace areas of hydroelectric
154 facilities, which can contain either unsuitable habitats (Cooke and Leach 2004,
155 Terraquatic 2011) or a much reduced area of potential spawning habitat (Chebanov
156 and Savelyeva 1999, Khodorevskaya et al. 2009, Zhang et al. 2013). Maintaining
157 existing connectivity is therefore preferred (see Rupert River case study) in the
158 absence of understanding the benefits accrued by migrating.

159 Fish passage offers a potential means to restore connectivity, however, sturgeon
160 have shown mixed results. Fish passage structures have typically been designed for
161 other species (e.g. salmonids) although use by sturgeon has been detected at some
162 facilities (Parsley et al. 2007). Sturgeon passage has also been detected via boat

¹ While this review focuses on the remediation of habitats in the vicinity of spawning areas we acknowledge that extended larval drift is a suggested requirement for some species {Zhuang, 2002 #198}{Kynard, 2007 #594}. In this review equating spawning and early rearing habitat is based on evidence of increased larval retention in response to substrate condition (e.g. Gessner et al. 2009; McAdam 2011; Crossman and Hildebrand 2014; Hastings et al. 2014). Prior studies have also shown that extensive drift by yolk sac larvae may be a response to unsuitable substrate conditions (see Gessner et al. 2009; McAdam 2011).

locks (Parsley et al 2002), fish elevators (Warren and Beckman 1993), although studies typically report low levels of passage. Recent studies (e.g. Kynard et al. 2011, McDougall et al. 2014, others) have begun to address sturgeon specific requirements for fish passage. The larger size of sturgeon and their benthic orientation present important design requirements (Jager et al. 2016, McElroy et al. 2012). For example, Thiem et al. (2011) found that lake sturgeon were often inhibited by turns within the fishway. Downstream passage presents another critical challenge as mortality associated with downstream passage may diminish the benefit of restoring upstream passage. The large size of adult sturgeon makes them particularly vulnerable to mortality during turbine passage. McDougall et al. (2014) showed that downstream passage survival rates vary depending on the passage route (e.g. turbines, spillway). Both upstream and downstream passage by white sturgeon in the lower Columbia River (Parsley et al. 2007) provides some hope that effective sturgeon passage is possible, but feasibility likely need to be evaluated on a case by case basis.

Flow restoration represents another remediation approach based on the association between sturgeon population declines and river flow regulation (Petts et al. 1989, Luk'yanenko et al. 1999, Gessner and Bartel 2000), Gessner et al. 2011. The positive correlation between freshet flows and recruitment (Nilo et al. 1997) and the tendency to spawn on the descending limb of the hydrograph suggest the importance of both the magnitude and pattern of freshet flows. Unfortunately the large scale anthropogenic changes that affect river flows (dams, floodplain abstraction, inland navigation) make full restoration challenging and possibly infeasible. In the absence of full restoration partial remediation requires a mechanistic understanding of how flow affects fish abundance, and in the absence of such knowledge it is uncertain whether partial solutions (e.g. the timing but not the full magnitude of historical freshet flows) will provide the desired outcomes. Beneficial effects of a conservation base flow in the Rupert River (see case studies) provide a recent example of positive outcomes of flow mitigation for a new project. Potential benefits of flow restoration for white sturgeon recruitment have also been suggested {UCWSRI, 2013 #383}. However, experimental flow restoration in the Kootenai River provided no detectable recruitment response (ref). Limited recruitment responses to naturally high flows in other cases (McAdam et al. 2005, McAdam 2015) suggest that flow alone may be insufficient to restore recruitment. Understanding the relationship between flow, sturgeon habitat and population responses is paramount to the design and implementation of effective flow remediation.

200

Dam operations can also affect reach scale conditions in spawning areas as a result of short term flow fluctuations (e.g. in response to short term changes in electricity

203 demand (Auer 1996b). Flow fluctuations have been associated with diminished use
204 by spawning adults (Auer 1996b), can result in eggs becoming stranded (Fisheries
205 and Oceans 2014; Gessner et al. 2011), and may stimulate larval drift (Crossman
206 and Hildebrand 2014). While the restoration of minimum flows is typically
207 considered one of the first steps in a flow restoration program(Auer 1996b)(Auer
208 1996b)Auer 1996b, site specific hydraulic models may be required to demonstrate
209 beneficial effects (Hildebrand et al. 2014).

210

211 The need for reach scale restoration reflects the effects of hydraulic conditions on
212 sturgeon spawning habitat selection location and reach scale fluvial
213 geomorphology. Altered hydraulic conditions in spawning habitats (Paragamian et
214 al. 2001, Zhang et al. 2009, Muirhead 2014) should be addressed during planning
215 stages of remediation works to ensure the utilization and maintenance of
216 remediated areas (see case studies). The dynamic nature of river channels (Church
217 1995) emphasizes that long term persistence of remediation works will require
218 detailed analysis of reach scale fluvial geomorphology in order to incorporate long
219 term channel changes at the project design stage. These considerations may be
220 most important for remediation in non-tailrace locations where there may be a
221 greater risk of underutilization if restored habitats are located in unsuitable areas
222 (e.g., Vlasenko 1974). It is also important to consider that manipulation of hydraulic
223 conditions in spawning reaches may provide an opportunity to concentrate
224 spawning in desired areas, or avoid others, however, such applications will require
225 an improved understanding of spawning habitat selection. Although the need for
226 reach scale considerations is recognized in recovery efforts for white sturgeon
227 (Nechako, Kootenay) and European sturgeon () we could find no current examples
228 of completed works at this scale.

229

230 For site specific remediation of spawning habitat identifying the location for
231 spawning habitat remediation a fundamental decision due to the uncertainty
232 regarding adult spawning site selection.. Consistent spawning at a well-defined
233 spawning site provides a straightforward means to define remediation sites,
234 although spawning is also known to persist in degraded spawning habitat
235 (e.g.,McAdam et al. 2005). For repatriation and recreation contexts, although
236 historical sites might be known or inferred, the degree of alteration since their prior
237 utilization increases the uncertainty regarding current suitability (Arndt et al. 2006).
238 While the construction of multiple sites may allow habitat selection by spawning
239 sturgeon, the potential impacts of dispersing spawners should be considered.
240 Fidelity to specific spawning sites (e.g.,Forsythe et al. 2012) suggests that the
241 natural tendency to aggregate in restricted spawning areas confers biological

242 benefits (e.g., mate choice) and restoration programs may need to consider
243 potential trade-offs if multiple restoration sites are planned.

244 Most successful examples of sturgeon spawning habitat remediation address lake
245 sturgeon spawning habitat in tailrace areas immediately downstream of dams
246 (Table 2). Such locations may increase the potential for success because the dam
247 creates a barrier to upstream movement that concentrates spawners immediately
248 downstream, spawning often occurs in consistent locations and fine sediments
249 inputs are limited. However, the area of available spawning habitat and may be
250 substantially reduced relative the extent of inaccessible upstream habitat (ref
251 Volga). Remediation at non-tailrace locations has shown limited success to date
252 due to limited use by spawning adults (i.e., limited egg deposition), or the
253 deposition of fines leading to decreased egg or yolk sac larvae survival (Table 2 and
254 case studies). Greater attention to reach scale hydraulic conditions and their
255 effects on spawning location and substrate will hopefully lead to improved success
256 for remediation in non-tailrace habitats.

257 Substrate augmentation has been the most common method for remediation of
258 sturgeon spawning habitats. This practice was initially based on the replication of
259 substrates found at natural spawning sites. More recently support for substrate
260 restoration has been based on links between substrate changes and recruitment
261 failure (McAdam et al. 2005, McDonald et al. 2010, McAdam 2015). Interstitial
262 habitats provided by gravel/cobble substrates are important for the retention and
263 survival of the egg and larval stages (Johnson et al. 2006b, Forsythe et al. 2013,
264 Crossman and Hildebrand 2014). The recent identification of strong egg adhesion
265 to multiple substrates (Parsley et al. 2013) suggests that substrate type has a
266 limited effect on egg retention. Additionally, (Johnson et al. 2006b, Forsythe et al.
267 2013) found that the position of adhered eggs is important, and interstitial eggs
268 showed decreased predation mortality relative to exposed on benthic substrate
269 surfaces. Similar findings also apply to yolk sac larvae (Gessner et al. 2009, McAdam
270 2011, Hastings et al. 2013) for which substrates with suitable interstitial habitats
271 increase larval retention (Crossman and Hildebrand 2014) and decrease both
272 predation and non-predation mortality (Gadomski and Parsley 2005a, McAdam
273 2011, Boucher et al. 2014). Recent identification of strong physiological benefits of
274 enriched substrates (Gessner et al. 2009, Boucher et al. 2014, Baker et al. 2015)
275 provides further evidence for the importance of interstitial rearing of yolk sac larvae.

276 The size and arrangement of placed sturgeon spawning substrates represents a
277 critical design decision, and placed substrates typically include both large diameter
278 materials to limit downstream displacement and smaller substrates that provide
279 suitably- sized hiding habitat. Previous spawning habitat restoration projects have
280 used 10-20 cm broken limestone (Bruch and Binkowski 2002, Roseman et al. 2011a,
281 Roseman et al. 2011b), 5-15 cm rounded igneous cobble (Manny et al. 2005) and 1-

282 5 cm coal cinders (Nichols et al. 2003, Thomas and Haas 2004). More recent
283 projects have used a mixture of substrate sizes (see case studies). Use of
284 substrates that are too large in diameter can limit the suitability for hiding by
285 yolk sac larvae leading to downstream displacement of larvae (McAdam 2011,
286 Terraquatic 2011). (Zhang et al. 2009) suggest that a 'pool and riffle' structure is
287 beneficial and enhances interstitial water flow, although under some circumstances
288 bottom relief may contribute to sediment deposition and infilling of interstitial
289 spaces. Infilling of placed substrates is ubiquitous challenge to the long term
290 maintenance of problem and greater input from the field of fluvial geomorphology
291 will be required to that ensure the long term sustainability of restored sites. Some
292 recent projects (e.g., St. Louis River see Aadland (2010); Rupert River see case
293 studies) have given greater consideration to design requirements, but future
294 monitoring will hopefully evaluate their long term effectiveness. In some cases
295 current flow regimes may not be competent to maintain such habitats, leading to
296 the need for either a) repeated physical cleaning or b) large scale engineering to re-
297 size the river channel for the regulated flow regime (McAdam et al. 2017). Such
298 large scale remediation works entail substantial cost and uncertainty, and will
299 require. In such toIn some large rivers it may be possible to locate sites below the
300 photic zone, as the growth of aquatic plants limited the effectiveness of
301 remediation works for lake sturgeon (Johnson et al. 2006b) (Gendron et al. 2002).

302 Locating restored habitats in existing or constructed side channels may circumvent
303 some of the challenges associated with mainstem locations, due to the potential for
304 natural or artificially diminished bedload (ref) but may increase limitations from the
305 perspective of site selection by spawning adults. In the extreme, use of off channel
306 habitats might entail physically moving spawners to enclosed off channel raceways
307 which might function similar to salmonid spawning channels. While early
308 experiences with this approach showed limited success (see (Chebanov et al.
309 2011), positive results were achieved with shortnose sturgeon (Kynard et al. 2011).
310 Factors such as fish size and the associated size of spawning channels as well as
311 captivity stress (Genz et al. 2014) may be important limitations of this approach.
312 Further research regarding spawning site selection would be highly beneficial for
313 evaluating off-channel remediation options. This might include the use of chemical
314 attractants to lure fish to novel spawning locations (see Sorensen and Stacey 2004).

315

316 **Monitoring Requirements**

317 Monitoring the effectiveness of habitat remediation is needed to ensure that
318 desired biological and physical responses are achieved. The duration of monitoring
319 programs should reflect the time scale of expected biological (e.g. juvenile
320 production, adult returns) and geomorphological (e.g. channel movement,

Comment [jg1]: Early Russian work in the 1950s focuses on such an approach before hormonal stimulation was used. Their results were poor with only 1 out of 10 fish maturing. Size and stress might be the main issues as well as the provision of proper substrate, temperature and flow).

substrate infilling) responses. Ideally, biological monitoring should demonstrate that habitat remediation is supporting all targeted life stages of sturgeon. We elaborate on these subjects in further detail below.

Biological Response

- i *Use by spawning adult sturgeon:* Use of restored habitats by spawning adults provides a straightforward metric of remediation effectiveness. Identification of spawning by sturgeon on restored habitat, ranges from the presence of deposited eggs to the number of spawners, sex ratios, and the density and depositional pattern of eggs. For example, recent genetic studies provide a means to estimate the number of spawning adults from collected wild progeny (Jay et al. 2014). Direct adult counts (see Rupert River case study) and both video (ref) and DIDSON acoustic camera (refs) have also been used to detect spawning adults. Evaluation of changes in spawning habitat use over time should also be considered in combination with physical monitoring discussed below. For the recreation and repatriation contexts the presence of spawning sturgeon on newly created habitats creates a special case of adult detection. Such cases may require sturgeon stray to novel spawning habitats. The potential that low straying rates could substantially delay the re-establishment of spawning runs emphasizes the long term nature of this metric. Cross-species comparisons and long-term research in controlled settings will also provide important reference studies of biological responses to construction of sturgeon spawning habitat (e.g., Forsythe et al. 2012, Pledger et al. 2013).
- ii *Early life stage survival and production of feeding larvae:* Monitoring should ideally demonstrate survival through the egg, yolk-sac, and feeding larval stages, though this is rarely done. Although quantifying stage-based survival may not be possible, systematic monitoring, using standard techniques such as egg mats, benthic sampling and drift nets, can be used to estimate total egg deposition (Caroffino et al. 2010), egg loss (Johnson et al. 2006b)), yolk sac larvae survival (Johnson et al. 2006b, McAdam 2012) and larval dispersal (Dumont et al. 2011, Crossman and Hildebrand 2014). Developmental staging of eggs or larvae to back calculate spawning time (Jay et al. 2014). Ontogenetic drift patterns (McAdam 2011) and larval quality indicators (Baker et al. 2015) also offer potential biological indicators. For example, drift by newly hatched larvae may be indicative of limited larval hiding in response to remediation (e.g., Khoroshko and Vlasenko 1970, Crossman and Hildebrand 2014).

Comment [JAC2]: In review in a different journal now, remove.

362 Ultimately, consistent monitoring of early life stages following
363 remediation of spawning habitat (possibly using multiple methods) is
364 one of the most important factors in determining remediation
365 effectiveness.

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367 iii *Juvenile recruitment*: Monitoring recruitment provides valuable
368 information and can be achieved through annual juvenile monitoring.
369 Gill nets have typically used for this application, although the delayed
370 vulnerability to gill net capture leads to a 2 to 3 year lag in
371 recruitment detection. Trawl nets have been also been used to
372 detect early juveniles (Parsley and Beckman 1994, Wanner et al.
373 2007), although the ability to use of trawl nets may be limited in
374 many applications (Steffensen et al. 2015).

375
376 iv *Use by non-target species*: While the main target of habitat
377 remediation is sturgeon, effects (positive or negative) on other
378 species also warrant consideration. For example, substrate
379 remediation may also benefit freshwater mussels (Haag and Williams
380 2014), macro invertebrates (Merz and Chan 2005, McManamay et al.
381 2013), salmonids (Jensen et al. 2009) and other lithophilic spawning
382 fish (e.g., Jennings et al. 2010, Romanov et al. 2012). The potential
383 for responses by non-target species to overwhelm responses from
384 target species (Pine III et al. 2009) must be seriously considered, and
385 supports the need broader monitoring programs. Sturgeon
386 recovery, and particularly repatriation in highly altered habitats (e.g.
387 *European sturgeon*), is often included within a broader suite of
388 ecosystem remediation objectives (e.g., KTOI 2009, Hondorp et al.
389 2014). While linking sturgeon remediation to broader habitat
390 remediation can yield important benefits, broadening recovery goals
391 may also increase the probability of not achieving sturgeon
392 restoration goals.

393 394 ***Physical Response***

395 i Channel structure: River channel responses to flow regulation occur
396 over decades or centuries (Church 1995), and long-term changes in
397 river channels may alter the effectiveness spawning habitat
398 remediation. Understanding fluvial and geomorphological processes
399 is a long term consideration that is important to consider during
400 project design and monitoring phases. River channels are dynamic
401 and it is important to ensure that remediation works are effective
402 despite long term changes in the river channel.

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429 Case Studies

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- ii Hydraulic conditions - The importance of hydraulic conditions to spawning habitat selection (Zhang et al. 2009, Du et al. 2011) underscores the need for pre and post-project monitoring to ensure that hydraulic conditions are maintained or enhanced. Detailed modelling (nhc 2008, McDougall et al. 2013, Hildebrand et al. 2014) and direct measurement (e.g. using ADCP; Elliott et al. 2004, Johnson et al. 2006a, Johnson et al. 2006b) have both been used to understand hydraulic responses. This aspect of physical monitoring is important to improve our understanding of spawning habitat selection at both the project design and monitoring stages.
- iii Substrate condition - Infilling of restored spawning substrates with fine sediments is a key concern for both short and long term effectiveness. Monitoring the effects of substrate (e.g. silt, sand or gravel) accumulation on remediated spawning habitat, and in other areas (e.g. downstream stretches, bank development, impacts on navigation), is a critical monitoring requirement. Monitoring techniques used to evaluate restored substrate quality have included video and diver observations of surficial characteristics and freeze-core sampling of river bed materials (Roseman et al. 2011a, Roseman et al. 2011b, nhc 2013a). Ideally assessments should develop a broad understanding of riverine sediment dynamics prior to remediation (e.g. sediment budget, spatial and temporal deposition patterns).

Sturgeon habitat remediation studies are not widely reported in the scientific literature and therefore four case studies are presented to provide examples across the range of remediation contexts and bio-spatial scales. The presentation of projects at various stages of implementation also illustrates both successes and limitations that should be beneficial to future projects.

Comment [s3]: Need to incorporate terminology introduced above re : context and bio-spatial scale into the case studies.

Feel free to make further suggestions.

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511 **White Sturgeon – Columbia and Nechako Rivers (context = rejuvenation, bio-**
 512 **spatial scale = spawning reach, spawning site)**

513 Recruitment failure of white sturgeon in both the upper Columbia and the Nechako
 514 rivers was not recognized until more than 30 years after it began. Both populations
 515 are listed as endangered in Canada and targeted restoration is required to prevent
 516 extirpation. River regulation and industrial use have led to altered flow regimes and
 517 habitat degradation over several decades. Spawning has been identified annually

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Comment [JAC5]:

Parsley, M. J., L. G. Beckman, and G. T. McCabe. 1993. Spawning and rearing habitat use by White Sturgeon in the Columbia River downstream from McNary Dam. Transactions of the American Fisheries Society, 122:217-227.

BC Hydro. 2015. Lower Columbia River Adult White Sturgeon Monitoring Program (CLBMON-28). Years 5 and 6 Data Report. Reported by BC Hydro, Castlegar, BC. 83 pp.

AMEC. 2014. Middle Columbia River White Sturgeon Spawning Monitoring Program (CLBMON-23a). Year 7 Data Report. Report Prepared for: BC Hydro, Castlegar. Prepared by: AMEC Environment & Infrastructure Ltd. 21 + 3 App.

for both populations over the past decade, though at differing spatial scales. In the Upper Columbia River spawning occurs at multiple locations (Howell and McLellan 2007, Ltd. 2008, Terraquatic 2011; BC Hydro 2015; AMEC 2014). Most spawning sites occur within a 75 km stretch of river and several are immediately downstream of hydroelectric facilities. In the Nechako watershed only one spawning site has been identified in a 2 km stretch of river (xx km downstream of Kenney Dam) where decreased river bed slope lead to the historical presence of gravel bars (now largely vegetated under the regulated flow regime). Spawning has been detected throughout the reach with activity concentrated in four areas which show locally elevated water velocity (McAdam et al. 2005, Triton 2009). Although historical spawning locations are unknown hydraulic modelling (nhc 2008) suggests that sturgeon spawned at a single site at the upstream end of the current spawning reach. For both the Columbia River and Nechako River the annual presence of wild spawners, coupled with the ability to implement experimental releases of early life stages (e.g. eggs and larvae) make these sites ideal settings to test the feasibility of spawning habitat remediation and determine the efficacy of different habitat remediation options.

Retrospective evaluations linking recruitment failure to substrate changes in white sturgeon spawning habitat (McAdam et al. 2005) (McAdam 2015) provide a strong foundation for pursuing substrate restoration as a means of population recovery in both rivers. Although bottom velocities at known spawning locations are within the suitable range (>1.0 m/s; Parsley et al. 1993), substrate surveys at several spawning areas show that high quality habitat is limited to a small proportion of surveyed sites (e.g. 3% - 12% in the Upper Columbia River; Golder 2013). Field studies in both rivers also demonstrate that larval catch is dominated by young yolk-sac larvae (Golder Associates Ltd. 2009, Terraquatic 2011) at most spawning sites, which also indicative of diminished quality of larval hiding habitat. Accordingly habitat requirements of early life stages (and particularly yolksac larvae) are used as the primary basis for designing spawning habitat remediation works that is a critical component of the federal recovery strategy for both populations (Fisheries and Oceans Canada 2014).

Experimental spawning habitat remediation has been tested at one site in the Upper Columbia River. Remediation focused on a small area of known egg deposition (1 km²) and the spawning substrate was modified with a combination of larger boulders (90% of material was 200-300 mm diameter) and coarse gravel (10% of material was 25-80 mm), both of which were angular in shape to provide more interstitial space when settled. The spawning habitat was located below the minimum water level to avoid dewatering eggs or larvae (Golder, 2011). The effectiveness of the restored habitat was tested by stocking yolk-sac larvae (~1 day post hatch) over both modified and control sites (inclusion of a control site is notable as suitable controls are often limited for such studies). Monitoring

559 demonstrated that larvae released over substrates with increased interstitial space
560 showed a greater tendency to hide, remained in the substrate regardless of the
561 flow conditions, and dispersed downstream volitionally (Crossman and Hildebrand
562 2014). Though successful in improving conditions, the modified spawning habitat
563 deteriorated rapidly within 2 years (J. Crossman, BC Hydro, unpublished data). The
564 highly variable flow regime in the study area resulted in the downstream
565 displacement of restored substrate, demonstrating the importance of thorough
566 evaluation of site specific hydraulics on substrate retention and maintenance prior
567 to construction.

568 At the Nechako River spawning site a large scale spawning habitat remediation
569 experiment consisting of the placement of 2,100 m³ of clean substrate was
570 undertaken prior to the 2011 spawning season. The mixture of large and small
571 material (see Table 2) was designed to achieve both physical stability and biological
572 function (i.e. interstitial habitat suitable for yolk sac larvae). While larval captures
573 have been limited the detection of small numbers of feeding larvae (n=XX) and wild
574 origin recruits (n=XX) from the 2011 year class (but not prior years) provides
575 evidence of a positive response to substrate remediation. The apparently limited
576 recruitment response may be due to the rapid changes to the enhanced substrates
577 that occurred due to an influx of sand over the majority of one gravel bed (bridge
578 site - nhc 2012). However, reach hydraulics appear to be limiting or delaying
579 further sediment infilling impacts and monitoring confirmed the maintenance of
580 biologically-functional substrate conditions in both 2012 and 2013 (nhc 2013a, b).

581 While experimental approaches in both rivers demonstrate the efficacy of substrate
582 remediation, further research regarding the geomorphology, substrate conditions,
583 and hydraulic properties of all spawning sites is required to design remediation
584 projects that maintain their effectiveness over the long term.

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754 **Conclusions**

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Our review of sturgeon spawning habitat restoration identified multiple contexts and bio-spatial scales that must be considered by remediation projects. Most remediation projects to date have been conducted at the sub-reach scale and have focussed on substrate remediation at specific spawning sites. The mixed success of past projects suggests that a 'build it and they will come approach' does not appear to have been highly successful. Increased success in the future will likely require a greater integration between the fields of biology and fluvial geomorphology. We see five main areas where further work would be beneficial.

- 1) Greater focus on fluvial geomorphological process (e.g. reach scale physical processes) in order to find ways to limit the incursion of fine substrates into restored spawning habitats. Finding ways to utilize the rivers own power are considered much more desirable than repeated physical cleaning that was employed by Johnson et al. (2006).
- 2) A further understanding factors that affect spawning site selection is required, including hydraulic conditions and fine scale habitat specificity (see Duong et al. 2011).
- 3) An improved understanding of habitat effects during early life history (e.g. survival, larval drift) and early juvenile phases. This should include a more nuanced understanding of habitat influences during all stages.
- 4) Both geomorphological and biological studies will necessarily require a combination of laboratory, modelled, and field studies. The high cost of large scale remediation emphasizes the important of evaluating past projects for other species.

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821 Table 1

822	<p><i>Mitigation:</i> In this context functional populations are present and the goal is to increase or maintain the availability and quality of sturgeon habitat. Mitigation implies confidence in the efficacy of spawning habitat remediation, but may be challenging for species with persistent biological uncertainty.</p> <p><i>Rejuvenation:</i> This category includes remediation of degraded habitats that continue to be used by spawning wild adults. For example, recent evidence (McAdam et al. 2005, Paragamian et al. 2009, McAdam 2015) supports the need for substrate remediation at spawning sites to address ongoing recruitment failures of white sturgeon. Even when contemporary spawning locations are known, ensuring the success of large scale remediation projects requires detailed information regarding spawning site selection and the biophysical properties that support recruitment.</p> <p><i>Re-creation:</i> Extensive habitat modification and destruction in some rivers leads to the need to create new spawning sites. Although adults are still present in such cases, complexity is elevated because suitable spawning locations and substrates may be unknown or assumed. Habitat re-creation requires knowledge about all life stages of sturgeon to ensure effective implementation and to diminish uncertainty regarding the recolonization and use of newly constructed.</p> <p><i>Repatriation:</i> Returning sturgeon to rivers from which they have been extirpated (e.g., European sturgeon) represents the most complex form of remediation and faces substantial uncertainty. Evaluation of the habitat capacity of recipient rivers (Gessner and Bartel 2000, Arndt et al. 2006) is challenging in the absence of sturgeon, particularly when habitat modifications have been extensive. For species for which remediation work is just beginning, substantial gains may be achieved by cross species comparisons.</p>
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Whole river scale: Long distance migrations are part of the life history of many sturgeons, and the negative effects of river impoundment on migration are widely recognized (Auer 1996a, Wei et al. 1997, Khodorevskaya et al. 2009). Large scale continuity of riverine habitat is also a suggested requirement for larval drift of pallid sturgeon (Braaten et al. 2012) and Chinese sturgeon (Zhuang, 2002 #198). Rivers also integrate multiple watershed scale processes creating the potential need for upland habitat restoration to diminish their secondary downstream effects (e.g. runoff and sediment budget effects of deforestation).

Reach scale: Within a selected river reach, spawning habitat selection is predominantly influenced by hydraulic conditions, with spawning generally occurring in higher velocity areas (e.g. > 1 m/sec; Parsley and Beckman 1994, Ban et al. 2011, Bennion and Manny 2014). Detailed evaluation of hydraulic conditions (Zhang et al. 2009, Du et al. 2011, Muirhead 2014) also suggests the importance of hydraulic elements such as turbulence, heterogeneous conditions and large roughness elements. Constant flow may also be important as flow fluctuations (i.e., peaking) downstream of dams can negatively affect spawning (Auer 1996b). Repeated spatial patterns of spawning habitat use in lake sturgeon (Duong et al. 2011) also suggest the presence of additional (undefined) preferences at the sub-reach scale.

Spawning sites: Links between recruitment failure and altered substrate conditions at spawning sites demonstrate the critical importance of benthic substrates to the proper functioning of spawning habitat (McAdam et al. 2017, Paragamian et al. 2009, Hastings et al. 2013). Negative effects of degraded substrates have been identified for eggs (Kock et al. 2006, Forsythe et al. 2013) and yolk sac larvae (Gadomski and Parsley 2005b, Gessner et al. 2009, McAdam 2011, Boucher et al. 2014). Impacts upon feeding larvae (e.g. diminished food supply) are also possible (Howell and McLellan 2011). While multiple attributes of spawning habitat have been described (e.g. depth, temperature) substrate is the attribute commonly addressed by remediation.

834 Table 1 Categories of uncertainty associated with different contexts for sturgeon spawning
835 habitat remediation.

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Uncertainty	Repatriation	Re-creation	Remediation	Mitigation
Recolonization	XX			
Habitat Use	XX	XX		
Habitat Suitability	XX	XX	XX	X

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Table 2

River	species	area (m ²)	velocity (m/sec)	depth (m)	material	Substrate depth (m)	Below dam (BD) / mid reach (MR)	Spawning (Y/N)	Year built	comments	references
Detroit and St. Clair (see table 4)	LS	39, 000	0.5-0.7	5-10	Various (see table 4; case study)	0.6	MR	N (Belle Isle), Y (other sites, some intermittent)	2004, 2008, 2012		Manny et al. 2005, Roseman et al. 2011; Thomas & Haas 2004, USGS 2014
Eastmain	LS						BD			Compensation for 890 m ² habitat impact	Environment Illimite (2009)
Kuban (upper)	Stellate ?	1.9 ha (check	0.76-0.84	4-6	5-8 cm, coarse sand, quarry stone	0.30	BD (80 m)	Y (1968)	1966		Khoroshko and Vlasenko (1974)
Kuban (lower)	STS SVS (CHECK	5 ha + 7.5 ha, K and V 1974 indicate 1.6 ha	0.88-0.94 m/sec	05-Apr	gravel, coarse sand, quarry stone		BD (900 m)	Y - silted after 3 years (check) according to Kerr et al	1966		Vlasenko 1974; Chebanov et al. 2008
Ottawa	LS				6-10 "		BD	TBD	2010/2012		Ron Threder pers. Comm.
des Prairies	LS	5, 000 and 8, 000	1.0	1.5-3.0	20-30 cm (area encircled with 30-50 cm rock)	0.3	BD	Y (also increased egg to feeding larvae survival)	1985, 1996	13 m ² /female recommended	Dumont et al. 2011 LaHaye et al. 1992
Ouareau	LS	3050	0.8 -1.2 (m/sec)	0.5-1.5 m	sedimentary blast rock and river rock (20-200 mm)	0.30 (min)	MR?	N - but check comments unclear	2007/2008	landslide affected quality of natural spawning site	LaHaye et al. 1990); MRNF-CARA. 2011. Restauration des frayères d'esturgeon jaune de la rivière Ouareau : sommaire du suivi biologique 2011. 7p + 1 annexes.

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Upper Black River	LS	4 locations	na	na	Rip rap	na	BD (<2 km)	na	1972	Sedimentation decreased effectiveness	Smith and Baker (2005)
Saint-Maurice	LS	2100			large boulder with 3- 40 cm material downstream	1 ??	BD - 2.5 d/s of Crabtree Dam	N - but present at nearby natural sites	2007-2011	COMPENSATION split into multiple small sites	(Faucher 1999, 2001).(GDG Conseil Inc. 2001)
St. Lawrence (Odensberg)	LS	36 x 36	na	4.3	4-7 cm	0.3	MR	Y (initially)	1993	Effectiveness decreased - siltation and zebra mussels	Johnson et al. (2006)
St. Lawrence (Iroquois)	LS	2 @ 929 m2	0.6-0.7	10-12	5-10 cm, large boulders d/s	0.30	above and below	Y	2007		McGrath 2009
St. Lawrence (Beauharnois)	LS	3000	0.46- 0.98 (also intermittent low flow events)	2.0 - 4.5	17 - 65 mm and 65 mm - 255 mm, with 1m x 5m blocks spaced at 8 m	0.30 (min.)	BD	N	1998	Ineffective due to siltation, vegetation unsuitable flow	Gendron et al. (2002)
St. Louis	LS	1,500 tons (200 truck loads)					BD	Y spawning, assessment limited to date	2009		Aadland pers. Comm, Aadland (2010)
Volga	RS?	~11,000	0.5-1.0	3-4	5- 10 cm		MR	rarely	1966	site too far d/s of dam	(Khoroshko and Vlasenko 1970)
Wolf / Fox	LS		up to 5 m/sec		rip rap		MR				Folz and Meyers (1985)
Columbia	WS	1, 000			2.5 to 30 cm (see case study)	0.60	BD	unconfirmed	2011	site degraded after 1 year	Crossman and Hildebrand (2014)
Nechako	WS	4,600		1- 3		0.30	MR	Y	2010	small recruitment response	Author's personal data; nhc 2013
Rupert	LS	2, 060	0.2 - 1.8	0.6 - 2.1	4 cm to 40 cm (see case study))	na	MR	Y	2010		Environment Illimité (2013)

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Figure 1

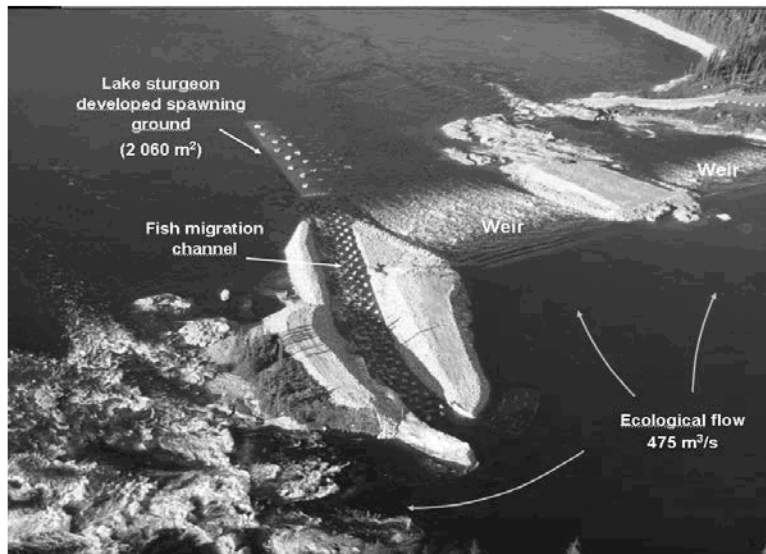


Figure 1. Areal View of the Lake Sturgeon Developed Spawning Ground at KP290 of Rupert River.

Figure 2 Results for larval monitoring in Rupert River

Figure 3 Map of the Upper Columbia River

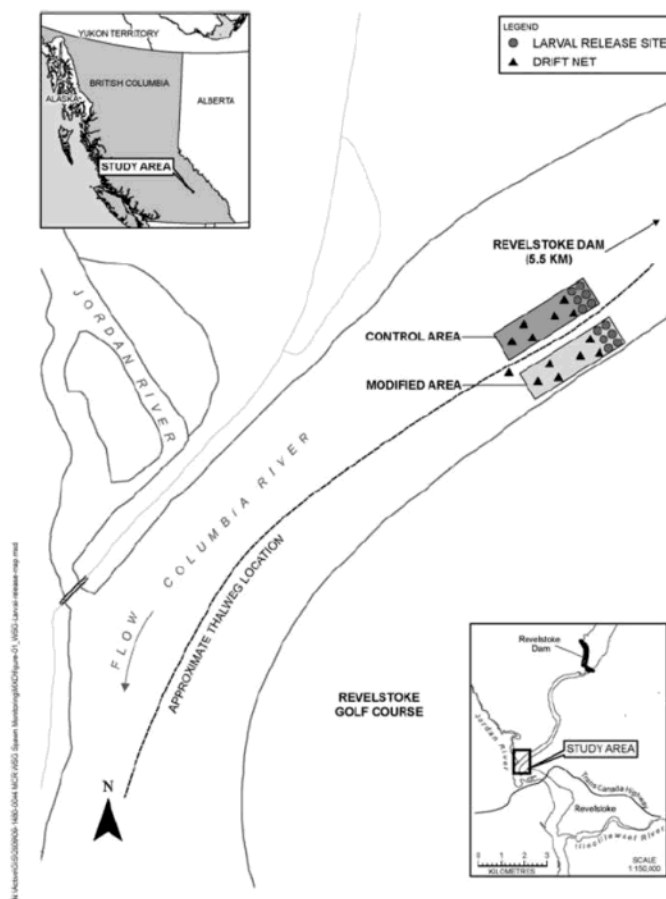


Figure 1. Map of the study site on the Columbia River near Revelstoke British Columbia showing the location of both the control and the modified sites and the drift net sampling design. Control and modified site dimensions measured 10 m in width by 100 m in length.

Figure 4 Crossman and Hildebrand figure re: larval retention

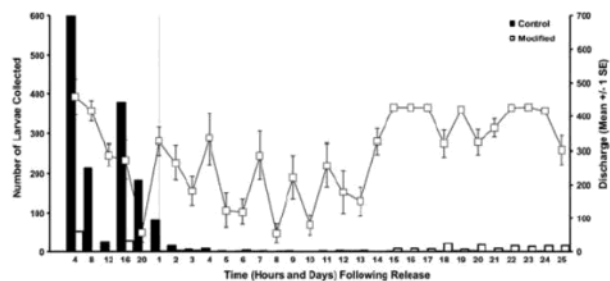


Figure 2. Number of larval white sturgeon collected at both control and modified sites by day with hourly discharge (cm) from Revelstoke Dam

Figure 5 map of Vanderhoof showing Nechako spawning locations and remediation sites (Cory can you add this in

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Figure 6. Map of the unobstructed Huron-Erie corridor (St. Clair River/Lake St. Clair/Detroit River) showing the locations of nine naturally-occurring, or restored, lake sturgeon spawning sites.

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Page 001 to/à Page 110

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