Identifying seasonal Lake Sturgeon (*Acipenser fulvescens*) movement patterns and habitat selection in the South Saskatchewan River Basin

by

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ABSTRACT

Lake Sturgeon (*Acipenser fulvescens* Rafinesque 1817) have experienced population declines throughout their range. In Alberta, low density age-class distributions, irregular recruitment, critically low spawning potential ratios and other factors led to a 2007 designation of "Threatened" for this species under the Provincial Wildlife Act. As a protected species, efforts to develop a comprehensive recovery strategy require an understanding of the species' biology, behavior, and critical habitat requirements. My objectives were a) to identify movement behaviors and habitat changes before and after an extreme flood event, and b) to ascertain overwintering movement behaviors and habitat selection of South Saskatchewan River Basin Lake Sturgeon. Multiple-receiver acoustic telemetry was used to obtain triangulated, fine-scale movement patterns at the confluence of the Bow and Oldman rivers (Grand Forks), a potential critical spawning habitat site, before, during and after an extreme flood, and at a study site on the South Saskatchewan River known to be critical overwintering habitat, before, during, and after the ice-on overwintering period. Substrate analysis was performed pre- and post-flood for Grand Forks, and substrate, bottom velocity, and depth analyses were performed for the South Saskatchewan River overwintering study site. In the extreme flood event study, movement behaviors were captured by receivers positioned to triangulate movements and provide positions at a fine scale. Receivers had been deployed to assess spawning behavior when the 2013 Alberta 'Flood of Floods' occurred, providing an opportunity to document fine-scale Lake Sturgeon movement behaviors before, during and after an extreme disturbance event. Lake Sturgeon showed a tendency to avoid high water velocity areas in favor of areas with lower water velocities. Increases in flow rate showed a significant negative relationship to mean positional distance from shore. Substrate assessment prior to and following the flood showed a significant change in substrate composition. Mean gravel- and larger-substrate area increased, providing evidence that high flow rates in 2013 and 2014 exposed larger particle fluvial substrate. Complexity as measured by patch density increased, indicating a measureable overall increase in heterogeneity. Lake Sturgeon benefitted from improved spawning habitat following the extreme flood by gaining larger, cleaner substrate with more complexity. Although extreme flood events may be costly to human life and infrastructure, they may be ecologically beneficial to some freshwater organisms, particularly plesiomorphic, long-lived species such as Lake Sturgeon whose survival has depended upon a capability to adapt to erratic and occasionally extreme peak flow events. In the overwintering study, fine-scale movements by adult and juvenile Lake Sturgeon were tracked for a previously identified overwintering habitat in the South Saskatchewan River using acoustic telemetry from late October 2013 through April 2014 for a 1.5 kilometer reach of the South Saskatchewan River identified in a previous study as overwintering habitat. Period-segmented movement rates, depth selection, aggregation behavior and preferential overwintering habitat selection by adult and juvenile Lake Sturgeon were evaluated for 23-26 individuals (20-23 adults and 3 juveniles, depending on residency during period assessed – individuals not present during all segments were excluded) detected within the study area. Environmental parameters included depth, depth standard deviation (rugosity), bottom velocity, bottom velocity standard deviation, and substrate type (silt, sand, and gravel or larger substrate). Boosted regression tree (BRT) analyses were performed to identify habitat selection for Lake Sturgeon for period-aggregated core (50th percentile) and range (95th percentile) positions. Movement rates paralleled temperature variation, becoming highly restricted during periods of deepest cold. Increased aggregation was also noted for these periods. The deepest habitat positions occurred during ice formation and breakup. Depth and bottom velocity were the most important variables used to identify sturgeon habitat for all periods assessed. Since Lake Sturgeon display site fidelity and aggregation behaviors independent of resource availability, winter habitat may limit the population. While spawning habitat is crucial to ensuring successful recruitment, data suggests that a substantial portion of the population spends the greater part of the year in overwintering locations, making this habitat potentially more critical to the survival of the population as a whole than any other habitat. If winter habitat is degraded or otherwise compromised, it could hinder species recovery, and should be considered critical habitat, receiving appropriate protection. This was the first study to use fine-scale acoustic telemetry analysis of movement behavior and habitat selection for a Lake Sturgeon population occupying fluvial winter habitat.

PREFACE

This thesis is an original work by Donnette Thayer. No part of this thesis has been previously published.

Study concept, field experimental design, surgical implantation of transmitters, and data collection were conducted as part of a research collaboration including Professor Mark Poesch at the University of Alberta, Douglas Watkinson at Fisheries and Oceans Canada (DFO), and Christine Lacho, then of the University of Lethbridge, currently of the North South Consultants Inc. Jonathan Ruppert, post-doctoral fellow at the University of Alberta provided guidance with data analysis. Mark Poesch was the supervisory author, and provided writing contributions to Chapter 2 of this manuscript, as did Douglas Watkinson (DFO) and Terry Clayton, Alberta Environment and Sustainable Resource Development (AESRD).

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This work would not have been possible without the expertise, innovation, and hard work of my supervising professor, Dr. Mark Poesch. It was Mark’s inspiration to study fine-scale fish behavior before and after the rare extreme flood described in Chapter 2, a extraordinary natural experiment that I found immensely exciting to study. Mark’s unique ability to combine vigorous action with deliberative sagacity has made him a rising star within the fish community, and I am forever indebted to him for taking a chance on me. Doug Watkinson offered continuous guidance throughout my program as a member of my committee, in addition to providing me with a dataset that made me the envy of my peers. He also dived the silty deeps of the South Saskatchewan River to ground-truth substrate, piloted the boat, gave me numerous reality checks on my substrate, bottom velocity and depth interpolations, and provided a vast amount of crucial guidance in all things fish. It was my good fortune to have the practical and informed direction and suggestions of Dr. Scott Nielsen, a valuable member of my committee, who applied to this work his talents as a gifted and meticulous scientist and first-rate writer. Christine Lacho’s fine “sturgery” work produced good signals from strong, healthy fish. She was a wonder in the field, careful, efficient, and tough. I thank Christine for introducing me to the only Lake Sturgeon I ever “met” in person, Fish #63336, who came up to say hello to us via a portable echosounder while we worked on the bank of the South Saskatchewan River at the study site. Emeric Janssens (AESRD) became a legend before I ever met him, having with his own two hands created some of the most effective receiver retrieval equipment I could imagine. I would like to thank Dr. Rene Belland, whose exhaustive and challenging class in Conservation and Management of Endangered Species provided me with indispensable insights regarding the intricacies and legalities surrounding methods of protecting our most vulnerable species, and Dr. Andreas Hamann, whose class in multivariate statistics formed the foundation of many of my statistical analyses. Jonathan Ruppert provided me with essential guidance in all of my advanced statistical analyses. His concrete suggestions and hands-on instruction provided me with a clear pathway that got me to the finish line. Terry Clayton’s exemplary fish knowledge and exceptional work protecting Lake Sturgeon was the driving force behind this and probably all other Lake Sturgeon work in Alberta. I am forever grateful to Terry and to the Lake Sturgeon Recovery Team for

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I was pleased to be part of a dynamic and engaging lab group, including Alli Banting, Karen Christensen-Dalsgaard, Cassandra Docherty, Kyle Hamilton, Bryan Maitland, Morag McPherson, Nate Medinski, Hedin Nelson-Chorney, Kenton Neufeld, Tyana Rudolfsen, Jonathan Ruppert, Nilo Sinnatamby, and Marie Veillard. You guys rock.

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Finally, I would like to thank all 123 Lake Sturgeon who participated in this study over the years, allowing us a glimpse into the lives of a truly extraordinary species.

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1.1 Species description

1.1.1 Overview

The Lake Sturgeon (*Acipenser fulvescens* Rafinesque 1817), one of 27 species within the family Acipenseridae, and one of five sturgeon species native to North America (Scott and Crossman, 1973; Grande and Bemis, 1996; Peterson *et al*., 2007; Barth *et al*., 2009). Native to the Mississippi, St. Lawrence (Great Lakes), and Hudson Bay drainages (Harkness and Dymond, 1961; Priegel and Wirth, 1971; Choudhury and Dick, 2001) and historically common in large North American rivers, the species has suffered considerable population declines (COSEWIC, 2006, 2007; Peterson *et al*., 2007; Pollock *et al*., 2015)..

Lake Sturgeon are a potamodromous, large-bodied, long-lived, benthic fish that retain numerous plesiotypic physiological and morphological characteristics, and exhibit protracted, intermittent spawning periodicity (Bruch and Binkowski, 2002). It is the largest fully fresh-water fish in North America (Rosenfield, 2002; Johnson *et al*., 2006), and the only potamodromous Canadian member of the family Acipenseridae (Scott and Crossman, 1973; Peterson *et al*., 2007). The longest specimen on record was a 125 kg fish reported to have a total length of 2740 mm, or 8.9 feet (Page and Burr, 1991). The heaviest on record was a 1943 capture from Lake Michigan with a confirmed mass of 141 kg and total length of 2410 mm, or 7.9 feet (Van Oosten, 1956; Peterson *et al*., 2007). The oldest documented Lake Sturgeon was estimated to be 153 years old, found in Lake of the Woods, Ontario in 1953 (MacKay, 1963). The largest Lake Sturgeon captured in Alberta prior to the current study was reported to have a mass of 47.7 kg, and total length of 1,549 mm (Winkel, 2000), though the current study includes a 1,601 mm specimen. The extremely large Lake Sturgeon specimens reported by Peterson and MacKay are now considered rare (Peterson *et al*., 2007).

1.1.2 Taxonomy and classification

Lake Sturgeon are members of the class Actinopterygii (bony fish), subclass Chondrostei (cartilaginous fish), order Acipenseriformes, family Acipenseridae, genus *Acipenser*. Currently, the family Acipenseridae includes four genera (*Huso*, *Acipenser*, *Pseudoscaphirhynchus*, and *Scaphirhynchus*) (Findeis, 1997; Nelson, 2006), and over 30 species (Bond, 1996; Peterson *et al*., 2007), though the actual number of modern species remains unknown as overfishing and habitat destruction had likely eradicated sturgeon populations before they could be identified (Birstein and Bemis, 1997).

1.1.3 Morphology

Members of the family Acipenseridae have heavy, elongate, fusiform bodies with cartilaginous skeletons, heterocercal tails, posterior dorsal fins, hyostylic jaw suspension, and spiral valve intestine. These features may have contributed to Linnaeus's classification of the first described acipenserid, the common or Baltic Sturgeon, *Acipenser sturio*, within the shark family (Linnaeus, 1758; Bemis *et al*., 1997). Five rows of bony scutes (modified ganoid scales) include a) a single dorsal row (9-17 scutes) extending from the skull to the predorsal scale of the dorsal fin; b) paired lateral rows (29-42 scutes) extending from the jaw to the base of the caudal fin; and, c) paired ventral rows (7-12 scutes) extending from the pectoral to the pelvic fins (Findeis, 1997; Peterson *et al*., 2003). Scutes are sharp and prominent during the juvenile stage (<30 cm), regressing into the dermal layer and becoming less pronounced with age (Findeis, 1997; Peterson *et al*., 2003; Peterson *et al*., 2007). Juveniles have several other distinct variations, including a noticeably upturned rostrum and dark dermal mottling. Adult coloration is monochromatic brown or gray, and off-white to white on ventral surfaces. Dermal denticles rather than scales cover the body (Scott and Crossman, 1973; Peterson *et al*., 2007). Lake Sturgeon show highly adaptive demersal characteristics; namely a counter-shaded, fusiform body with dorsal ventral compression and large pectoral fins to aid station-holding ability, and a protractile, inferiorly-positioned, toothless mouth preceded by four sensory barbels for benthic foraging (Peterson *et al*., 2007). Barbels possess chemical sensory systems functionally similar to taste buds (Collin, 2007), as do the lips and interior of the mouth (Kasumyan, 2011).

While overall phenotypic variation is limited, sturgeon show a high rate of body-size adaptation. Body size ranges from Dwarf Sturgeon (*Pseudoscaphirhynchus hermanni*), with a maximum confirmed total length of 275 mm (Robins *et al*., 1991), to Beluga Sturgeon (*Huso huso*), with a maximum confirmed total length of 8,000 mm (Kottelat and Freyhof, 2007). For comparison purposes, body sizes of Lake Sturgeon in this study ranged from 626 mm to 1601 mm when tagged. Acipenseridae body size evolution rates were 5.4 times higher than body size evolution rate for all other lineages assessed in one study (Rabosky *et al*., 2013).

1.1.4 Life history

Lake Sturgeon display late maturity and intermittent spawning, slow growth, low recruitment rates (Haxton and Findlay, 2008) and high egg mortality rate (Forsythe *et al.* determined a 91% mortality rate at 80% incubation) (Forsythe *et al*., 2013). Female Lake Sturgeon begin spawning between the ages of 18 to 27 years, males between the ages 12 to 15 years (Bruch and Binkowski, 2002; Peterson *et al*., 2007). Females spawn once every 4-7 years, males once every 2-4 years (Auer, 1999; Forsythe *et al*., 2012), presumably to optimize fecundity – numerous researchers have identified a strong correlation between body mass and fecundity (Harkness and Dymond, 1961; Auer, 1999; Bruch *et al*., 2006), and Lake Sturgeon are among the most fecund of all North American freshwater fishes (Harkness and Dymond, 1961; Scott and Crossman, 1973; Peterson *et al*., 2007). While Lake Sturgeon's late sexual maturation and large body size at first spawning and consequent elevated fecundity may have once contributed to its evolutionary success, this adaptation now limits population recovery (Peterson *et al*., 2007; Cleator *et al*., 2010; DFO, 2010).

Though their entire life-cycle occurs in fresh-water, Lake Sturgeon perform seasonal migrations to spawning, feeding, and overwintering locations (Auer, 1996), and some populations show a high degree of site-fidelity (Lyons and Kempinger, 1992; Auer, 1996). One individual in this study had a maximum migration range of 687.8 river kilometers, the second highest range recorded for Lake Sturgeon (Lacho, 2013).

Lake Sturgeon have remarkable plasticity in their dietary choices, enabling the species to exploit a wide range of food resources (Pollock *et al*., 2015). Generally Lake Sturgeon are considered to be indiscriminate carnivores consuming whatever small benthic prey is available (Lebreton and Beamish, 2004), and take the role of a general predator in resource-poor conditions (Beamish *et al*., 1998). While the majority of the Lake Sturgeon diet consists of macroinvertebrates (amphipods, chironomids, and mollusks) (Scott and Crossman, 1973; Kempinger, 1996; Lebreton and Beamish, 2004), small fishes such as sculpins and sticklebacks are also consumed (Lebreton and Beamish, 2004). Zebra Mussels were identified as the dominant food source for New York's Oneida Lake Lake Sturgeon whose total lengths exceeded 900 mm (Jackson *et al*., 2002), and a deliberate preferences for Zebra Mussels was found among individuals exceeding 700 mm for zebra mussel-dominated habitat (Boase *et al*., 2014).

1.1.5 Natural history

Members of the order Acipenseriform have undergone few evolutionary changes since the Cretaceous period (Figure 1-1) (Bemis and Kynard, 1997; Choudhury and Dick, 2001; Peng *et al*., 2009; Betancur-R *et al*., 2013), diverging from Polyodontidae (paddlefish) during the Jurassic period between 180-100 million years ago, probably in association with the separation of North and South America (Grande and Bemis, 1996; Bemis *et al*., 1997; Peng *et al*., 2007; Peng *et al*., 2009; Betancur-R *et al*., 2013). Sturgeon's retention of plesiotypic characteristics is well-documented; many researchers note the difficulty distinguishing Acipenser fossil taxa from living taxa (Woodward and Sherborn, 1890; Woodward, 1895; Wilimovsky, 1956; Bemis and Kynard, 1997; Hilton and Grande, 2003). The species' relict characteristics include its cartilaginous skeleton, heterocercal caudal fin, open, unregulated swim-bladder, and dermal denticles rather than scales (Watanabe *et al*., 2008; Halvorsen *et al*., 2012). Acipenserformes and undifferentiated Chondrostei precursors first appeared in the fossil record in the late Jurassic to early Cretaceous period (208–146 million years ago) (Gardiner, 1984; Peng *et al*., 2009;

Brinkman *et al*., 2013), and are one of only two Chondrostei orders to survive within the Actinopterygii class, Acipenseridae (sturgeons) and Polyodontidae (paddlefishes) (Betancur-R *et al*., 2013).

1.2 Scientific interest in Lake Sturgeon

Study of Acipenseriformes has recently increased. Given the relatively continuous fossil record (Hilton and Grande, 2006) and availability and variety of surviving species for study (sturgeon make up approximately 50% of extant species of the plesiomorphic Chondrostei infraclass), Acipenseriformes present a compelling outgroup for molecular phylogenetics studies, providing insight into genetic variations in comparison to other fishes with Chondrosteidae roots, including fishes in the Actinopterygian and Osteichthyan classes (Grande and Bemis, 1991). As a large, bottom-feeding fish, they have shown importance as an environmental indicator species (Casselman *et al*., 1999; Lagutov, 2008), reflecting riverine health at both a large-scale (body size requires commensurately large, unfragmented, undegraded habitat) and a small-scale (sturgeon eggs, fry, and young-of-the-year (YOY) are vulnerable to predation and habitat loss (Kynard *et al*., 2005; Bruch *et al*., 2006; Alberta Lake Sturgeon Recovery Team, 2011)).

1.3 Conservation status

Lake Sturgeon have been identified as a globally and nationally vulnerable species (G3, N3) (NatureServe, 2013) believed to be at risk throughout their range (Peterson *et al*., 2007), though recent conservation efforts have been effective in restoring populations in some regions and the species designation has been downgraded at a global level to Least Concern (IUCN, 2015). Federally, the species is under consideration for addition to Schedule 1 of the Species at Risk Act (Alberta Lake Sturgeon Recovery Team, 2011; Pepper, 2012; COSEWIC, 2014). Legal Lake Sturgeon harvest in Alberta was discontinued in 2004/2005, and remains catch-and-release only (Alberta Lake Sturgeon Recovery Team, 2011). Alberta Lake Sturgeon reside in Designatable Unit 2 (DU2) (Figure 1-2), a management unit defined by aquatic ecozone and genetic similarity, this includes the North and South Saskatchewan rivers and their tributaries and spans eastern Alberta, Saskatchewan, and a small portion of western Manitoba. In December 2007, the DU2 Lake Sturgeon population was listed as "Threatened" (equivalent to IUCN "Imperiled") in Alberta under the Wildlife Act (Alberta Lake Sturgeon Recovery Team, 2011). The study population is defined within Designatable Unit 2 (DU2), Management Unit 2 (MU2) (DFO, 2010). DU2; MU2 includes the lower Red Deer, Bow and Oldman rivers, and the South Saskatchewan River downstream to Gardiner Dam that created Lake Diefenbaker (Figure 1-2) (Alberta Lake Sturgeon Recovery Team, 2011). Population estimates for the South Saskatchewan River averaged 6,400 catchable fish between 2003 and 2009, with the caveat that obtaining quantitative Lake Sturgeon population estimates in the North and South Saskatchewan rivers remains a stated goal (Alberta Lake Sturgeon Recovery Team, 2011).

1.4 Threats to Lake Sturgeon populations

1.4.1 Threats to general populations

Initial population declines resulted from overexploitation, which is still a concern. Currently, waterway fragmentation is the dominant threat to Lake Sturgeon populations, in combination with exploitation, and habitat loss, and degradation (Figure 1-3). Examples of diminished habitat include reduced and regulated river flows, degenerated water quality, introduction of agricultural, industrial, and municipal contaminants, dikes and dams that hinder migration, backwater riverine area reduction via channelization and stream desiccation, habitat loss due to reservoir creation, and removal of spawning grounds to further urban development (Harkness and Dymond, 1961; Boreman, 1997; Haxton and Findlay, 2008; Pollock *et al*., 2015).

1.4.2 Threats to DU2/MU2 population

Over-harvest, both historical and contemporary (via poaching), is a prominent threat to this population. The 2002 report on the status of the Lake Sturgeon (Acipenser fulvescens) in Alberta suggested a 20% mortality rate for this population based on harvest alone (Earle, 2002). Other threats to the South Saskatchewan River population include competition with stocked and invasive species, fragmentation from dams, dikes and weirs, alterations in flow regime, droughts arising from climate change, and anoxia resulting from eutrophication (Table 1-1). Threats include unidentified stressors, including extreme disturbance events (e.g. large floods), have not yet been fully studied, and encompass identified threats (e.g. habitat destruction) within critical habitat (e.g. overwintering habitat). These are listed as items of concern in the Knowledge Gaps And Research Priorities section of the Alberta Lake Sturgeon Recovery Plan (Alberta Lake Sturgeon Recovery Team, 2011).

1.5 Study goals

To address knowledge gaps cited in the Alberta Lake Sturgeon Recovery Plan 2011-2016, two studies were undertaken to analyze and document 1) the impact of disturbance in the form of a large flood on Lake Sturgeon spawning habitat, and fine-scale movement responses of sturgeon during periods of extreme peak flow. This addresses knowledge gap 4.4, Threats (Alberta Lake Sturgeon Recovery Team, 2011), specifying the need for information on stressors; and 2) overwintering movement rates, depth selection, aggregation behavior and habitat selection by adult and juvenile Lake Sturgeon, this addresses knowledge gap 4.1, Biology (Alberta Lake Sturgeon Recovery Team, 2011), specifying the need for studies regarding winter distribution. Both study goals address knowledge gap 4.2, Habitat (Alberta Lake Sturgeon Recovery Team, 2011), specifying the need for an understanding of seasonal distribution and habitat use, critical to achieving judicious habitat protection within the context of sensible economic and commerce objectives.

1.6 Tables

Table 1-1. Primary threats to South Saskatchewan River Basin Lake Sturgeon population. Modified from the Alberta Lake Sturgeon Recovery Team (2011).

Threat	Detail	Concern
Direct		
Exploitation	Illegal (poaching)	Removal of adult fish diminishes the population and reduces the number of reproducing individuals
Species Introduction	Non-native fish	Predation by stocked species on eggs and fry
Indirect		
Fragmentation	Dams, weirs, hydroelectric facilities	Halt migration to spawning, feeding or overwintering sites, problematic for high site-fidelity fish species
Habitat Degradation	Changes in flow	Reductions in flow degrade spawning habitat quality; may negatively impact seasonal migration cues
	Water extraction	Impede migration to spawning, feeding or overwintering sites
Climate Change	Increased chance of natural disturbance; increase likelihood of water extraction	Warmer temperatures increase evapotranspiration, reducing surface water availability and increasing municipal water use; increased flow regime alterations, increased likelihood of intense, long-lasting droughts
Pollution	Irrigation returns	Eutrophication leading to anoxia

1.7 Figures

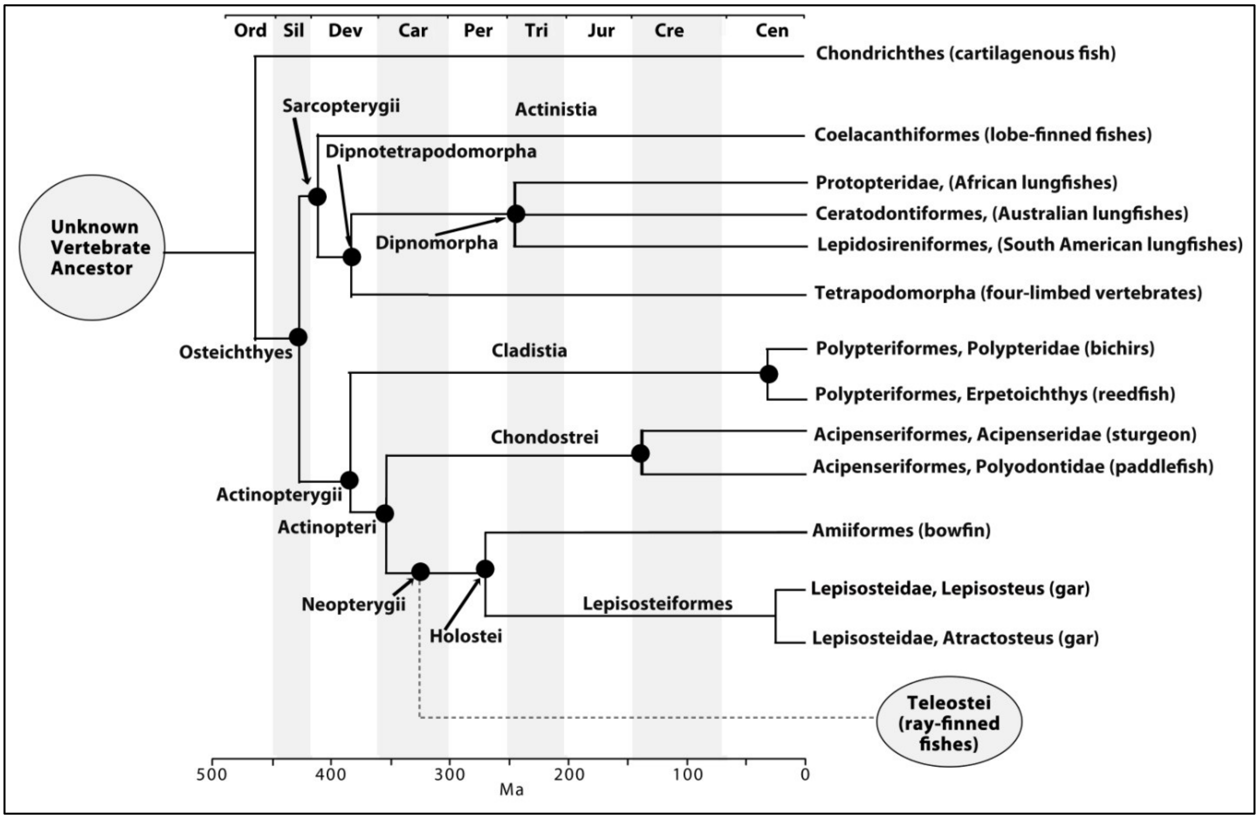


Figure 1-1. Phylogenetic tree. Developed using RAxML 3+ dataset, highlighting relict fish species. Adapted from Betancur-R *et al.*, (2013) (Betancur-R *et al.*, 2013).

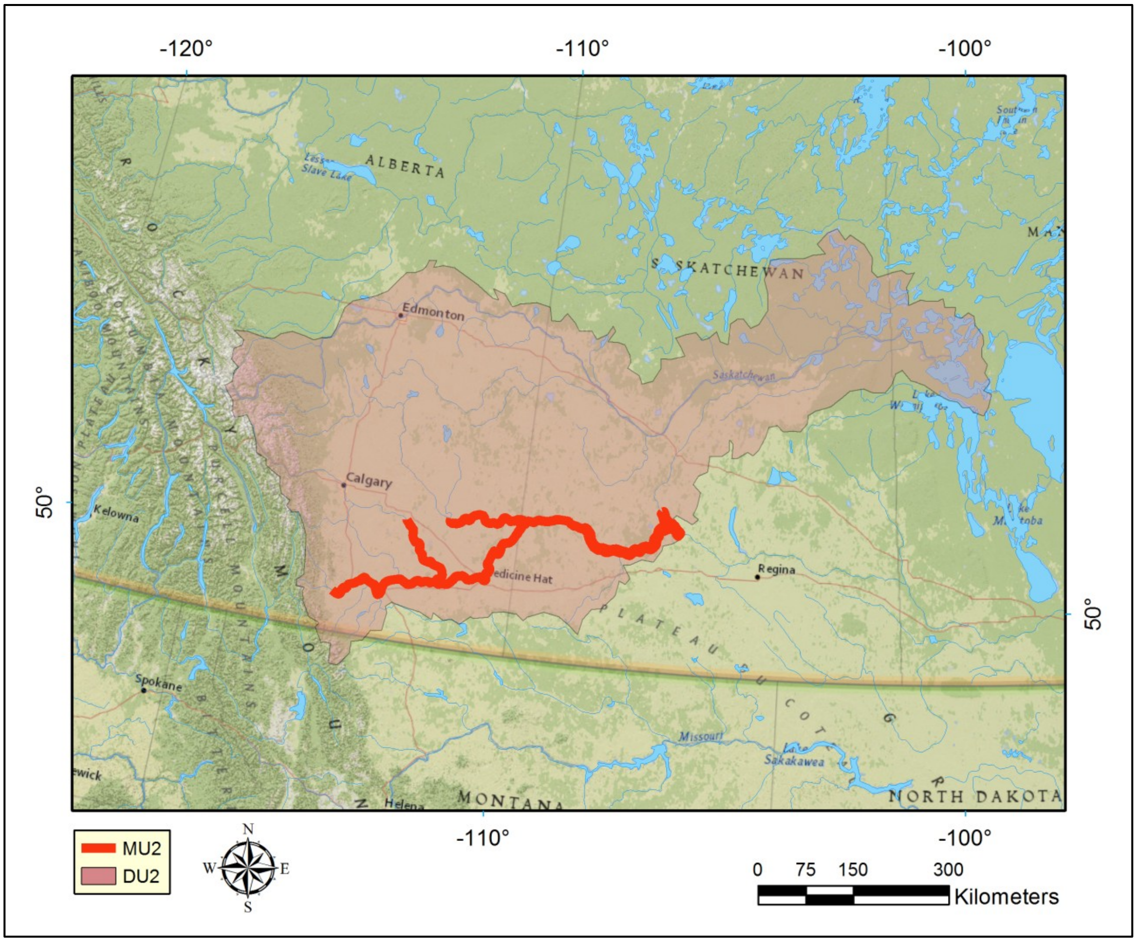


Figure 1-2. Designatable Unit 2 (DU2) Management Unit2 (MU2) within the North American Lake Sturgeon distribution (COSEWIC, 2006).

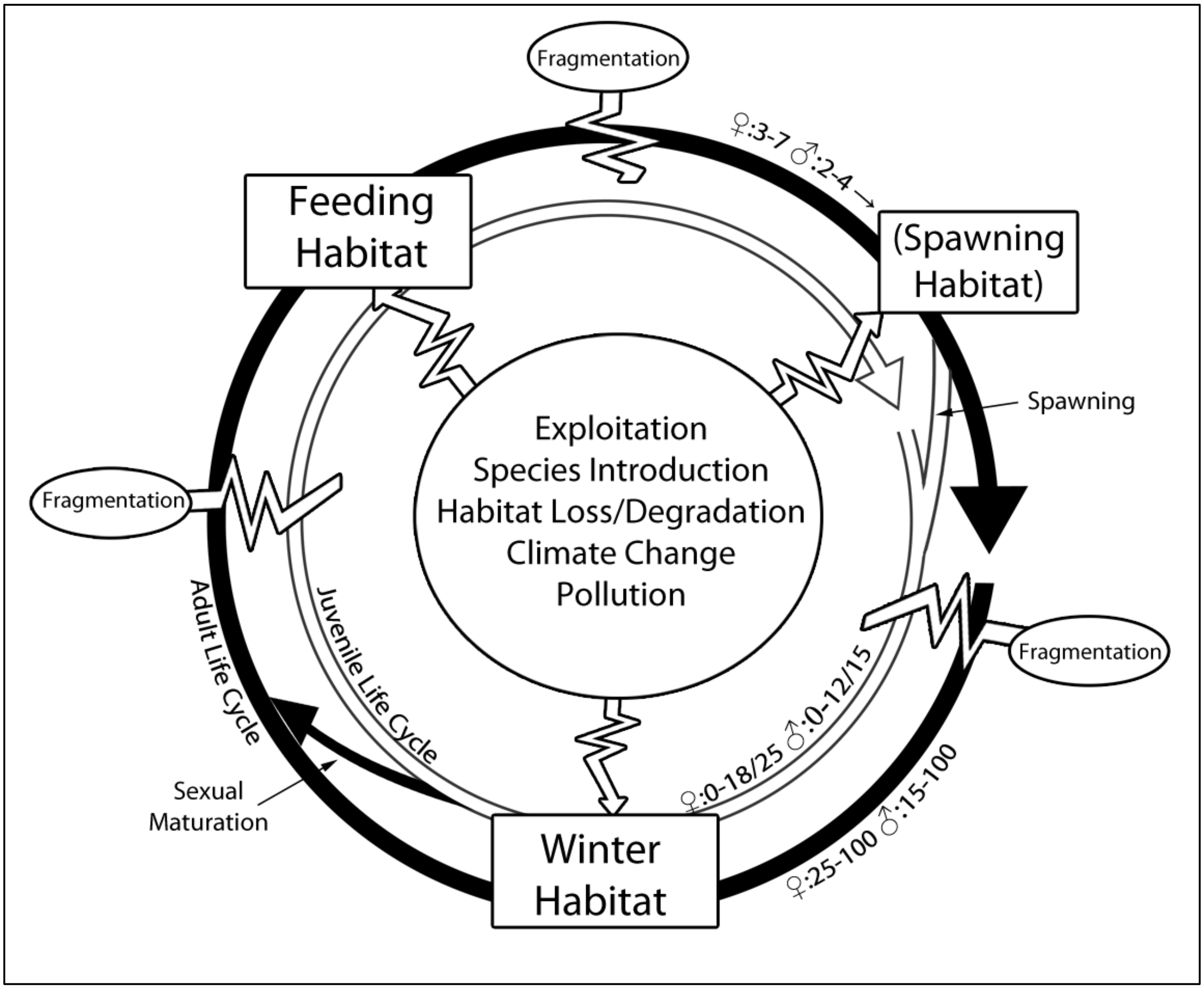


Figure 1-3. Lake Sturgeon life cycle and threats identified prior to current analyses (Alberta Lake Sturgeon Recovery Team, 2011). Pre-adult life cycle/stage (spanning 0 years to sexual maturation between 18 to 25 years for females, 12 to 15 years for males) is indicated by the white inner circle, adult life cycle/stage (spanning 25 to 100 years for females, 15 to 100 years for males) is indicated by the black outer circle. Spawning habitat is enclosed in parentheses to indicate individuals do not spawn every year. Females spawn once every 3 to 7 years, males once every 2 to 4 years (Auer, 1999). Key life history transitions (sexual maturation and spawning) are indicated by paths crossing between the black and white circles. Threats are indicated by crooked lines and arrows. Data regarding threats for this populaton were primarily drawn from the Alberta Lake Sturgeon Recovery Plan (Alberta Lake Sturgeon Recovery Team, 2011). See Table 1-1 for details.

Chapter Two: **Swimming against the flow: Habitat alteration and avoidance behavior of Lake Sturgeon (*Acipenser fulvescens*) during Alberta, Canada's 'Flood of Floods'**

ABSTRACT

Large scale ecological disturbances such as extreme floods are expected to increase due to climate change (Running, 2008). In 2013, central Alberta, Canada, received the largest flood in contemporary history, which displaced over 100,000 people and is known colloquially as Alberta's 'Flood of Floods.' Flow rates in the Bow River peaked at 3,320 m^3/s, the highest flow on record, more than double the previous record. A study of the relationship between habitat and fine-scale movement of Lake Sturgeon (*Acipenser fulvescens*) was underway in the Bow and Oldman rivers when the flood occurred. Rare, fine-scale movement behaviors were documented under extreme flood conditions. Lake Sturgeon showed a tendency to avoid areas in the water channel with the highest flows. For example, increases in flow rate showed a significant negative relationship to mean positional distance from shore ($r= -0.654$, $p<0.001$, $n=45$). Substrate composition significantly changed pre- and post-flood. There was a significant increase in the mean area of gravel and larger substrate, providing evidence that high flow rates in 2013 and 2014 exposed larger particle fluvial substrate. Post-peak 2014 complexity as measured by patch density increased significantly from pre-peak 2013 complexity, suggesting that the removal of silt exposed varying patterns of more complex and substantive underlying rocky substrate. Here, we show a clear benefit for Lake Sturgeon spawning habitat following the extreme flood: larger, cleaner substrate with more complexity. Although extreme flood events may be costly to human life and infrastructure, they may be ecologically beneficial to some freshwater organisms, particularly plesiomorphic, long-lived species such as Lake Sturgeon, which show avoidance behavior during such extreme events and improvement in habitat.

2.1 Introduction

Ecological disturbances, such as droughts, floods, fires, storms and disease outbreaks, are often characterized by their ecological impacts on population size, species diversity, and redistribution of ecosystem resources across a broad spatial and temporal range (Lytle and Poff, 2004). In aquatic ecosystems, floods have been linked to a variety of both positive and negative effects including extensive alterations in population assemblages and trophic structure (Jensen and Johnsen, 1999), and the regulation of population dynamics (Junk and Piedade; Meffe, 1984; Jensen and Johnsen, 1999; Vincenzi *et al*., 2012). During normal conditions, floods can contribute an important yearly influx of nutrients and organic materials (energy) that supports freshwater fish communities.

Impacts of extreme floods, those that occur rarely (e.g. 1:100 years), on aquatic organisms are variable and poorly understood. Sessile species (plants), meiofaunal invertebrate species (nematodes), or motile species with inflexible bodies (mollusks) may experience mortality and extensive displacement during extreme floods (Reice, 1985; Matthews, 1986; Palmer *et al*., 1992). New sediment build-up can result in mortality to macroinvertebrates, damage to mouth parts or gills of fish, alteration of habitat and refugia, and turbidity-related growth reductions in light-deprived algal food sources resulting in starvation mortality in primary producer macroinvertebrate scrapers and grazers, and commensurate resource deficits up the food chain (Cordone and Kelley, 1961; Rosenberg and Wiens, 1978; Newcombe and Macdonald, 1991).

The impacts of extreme floods can have cascading effects on ecosystem function. Invasive aquatic species can be less resistant to extreme peak flow events than are native species (McMahon, 2002) providing a competitive advantage for some species. Meffe (1984) found the Gila Topminnow (*Poeciliopsis occidentalis*) capable of surviving desert flash floods that extirpate its primary competitor, the invasive Western Mosquitofish (*Gambusia affinis*). Anthropogenic-related reductions in the magnitude and frequency of floods have been correlated to population decline in a number of Pacific salmon species (Waples *et al*., 2009) and other migratory fishes. Re-establishing flood regimes in regulated rivers has been suggested as a method to recover depressed populations of native fish species (Stanford *et al*., 1996).

The initial objective of this study was to assess the fine-scale spawning movement of Lake Sturgeon (*Acipenser fulvescens*) relative to substrate and other habitat factors in the Oldman and South Saskatchewan rivers in Alberta, Canada. This area is suspected to be important spawning habitat for Lake Sturgeon populations (Lacho, 2013), and has been designated as sensitive habitat (Alberta Lake Sturgeon Recovery Team, 2011). Loss of spawning habitat resulting from fragmentation, habitat loss, and diminished water quality is a primary driver of Lake Sturgeon population declines across the majority of its range (Tody, 1974; Auer, 1996; Chiotti *et al*., 2008). Therefore, understanding spawning habitat selection is critical to mitigation of spawning habitat and nursery area reductions associated with reduced population size.

Concurrent to the deployment of receivers to position fine-scale movement along the Oldman River and its confluence with the Bow River, the largest recorded flood event occurred across the 32 consecutive years of monitoring Bow River flows. Peak flows rose by 1,850 m^3/s in a single day, increasing from 1,470 to 3,320 m^3/s on June 23, 2013 (Alberta, ND). By comparison, this flood was more than twice the previous record of 1,530 m^3/s, and was known colloquially as “Alberta’s Flood of Floods.” The flood claimed the lives of four people, displaced over 100,000, and was the most expensive disturbance event for insurance claims in 2013 in North America (Swiss Re Ltd., 2014). The fine-scale positioning study allowed for an assessment of behavior of Lake Sturgeon before, during, and after the flood. Given the paucity of data on fine-scale freshwater fish behavior during floods, the subsequent objectives of this study were to investigate *in vivo* Lake Sturgeon movement patterns in relation to this extreme flood event, and to discern the role of such events on habitat.

2.2 Materials and Methods

Fine-scale habitat and movement data were collected from seven study sites across an approximately 20 kilometer reach near the confluence of the Oldman and Bow rivers in southern

Alberta, Canada (Figure 2-1). The Oldman River flows roughly west to east, originating in the Rocky Mountains and passing through the foothills and plains of southern Alberta before its confluence with the Bow River to form the South Saskatchewan River. These rivers are typically slow, meandering prairie waterways with highly incised channels and large seasonal fluctuations in flow. A total of 123 Lake Sturgeon were surgically implanted with VEMCO V16, 69 kHz transmitters in 2010 and 2011. Transmitter battery life was approximately five years with an average transmitter delay of 120 seconds. At capture, fish total length ranged in size from 626-1601 mm (mean = 1112 mm). Forty-five individuals entered the study area during the study period; 43 were detected in the fine-scale arrays with more than one position.

2.2.1 Habitat assessment

Substrate data were collected during base flow conditions in 2013 and 2014 using a single beam 200 kHz transducer with nine-degree beam angle emitting 5.0 pulses per second for 0.4 millisecond per pulse (MX Aquatic Habitat Echosounder, BioSonics, Inc., Seattle, Washington, U.S.A.). Hydroacoustics uses a series of acoustic pulses to determine substrate hardness and type. Pulses travel through water at an approximate speed of 1,500 meters per second, reaching the river bottom or another solid object, and are reflected back toward, and are received by, the transducer. Signals exceeding a threshold level are identified on the echogram, and their travel time is used to calculate range (distance from the transducer). Echo amplitudes are then used to discern substrate types (Burczynski, 2002). Visual Habitat software (BioSonics Inc., 2013) was used to conduct bottom detection analysis with a bottom echo of 1 and 3 times pulse lengths for part one and two echoes respectively, a fractal dimension threshold of -60, energy filter set at 5 pings (averaged), with an energy threshold of 75%.

A fuzzy c-means clustering analysis was performed to derive substrate classifications (Bezdek *et al*., 1984). Fuzzy clustering is an unsupervised machine learning algorithm that identifies patterns in data, and is comparable to unsupervised classification methods used to categorize large-scale land-cover types (Foody and Cox, 1994; Zhang *et al*., 2014). Fuzzy cluster memberships have correlated strongly with actual memberships identified independently (Foody and Cox, 1994; Zhang *et al*., 2014). Though training data are not explicitly required for fuzzy cluster analysis (Tyagi *et al*., 2005; Masalmah and Velez-Reyes, 2006; Miao *et al*., 2007; Yang *et al*., 2010), visual validation was performed using high-resolution (1.296 m/px) satellite imagery for the period (Cablk and Minor, 2003; Fonstad and Marcus, 2005; Google Imagery and Digital Globe, 2015), and through geo-referenced photography of substrate. To further validate bottom typing, bathymetry interpolations were performed for both years, and relative bathymetry was used to define substrate classes.

Substrate classifications were loaded into ArcMap, and subsetted into shapefiles for each year and array. Euclidean allocation (Locker *et al*., 2010) was used to identify and interpolate natural groupings of sampled points (cell size = 1 m^2). Regions with data for both years were extracted and a two-way analysis of variance was used to evaluate overall change in substrate composition, using substrate and year as effects. This analysis was completed using the R programming language v.3.1.2 (R Core Team, 2014).

Patch density analysis was used to assess differences in the spatial aggregation of Lake Sturgeon habitat pre- and post-extreme the flood event. Patch density analysis is a technique that has been used to measure terrestrial landscape fragmentation (Hopkins and Whiles, 2011), and is increasingly used in aquatics to assess riparian areas (Johnson *et al*., 1997). Patch density (PD) was calculated as:

$$PD = \frac{PN}{A} \text{ X } (10{,}000) \text{ m}^2\text{/ha X } 100 \qquad (1)$$

where A = total substrate area (m^2) by array

and $$\text{PN} = \sum_{i=1}^{n} p_i \qquad (2)$$

where, p_i = patches in array.

2.2.2 Behavior assessment

Fish behavior was assessed using acoustic telemetry surveys of fish movement. VEMCO™ (VR2W-69 kHz) receivers were configured in VEMCO Positioning System (VPS) arrays to allow for triangulated data to be collected at a fine scale. Six VPS arrays were placed along the Oldman River, and one array in the South Saskatchewan River at the confluence of the Oldman and Bow Rivers (Figure 2-1). The array locations included substrate suitable for Lake Sturgeon spawning: shallow, rocky riffles with greater than average water velocities. Spawning activity observed at this location led to its designation as Class A habitat by the Alberta Lake Sturgeon Recovery Plan team (Alberta Lake Sturgeon Recovery Team, 2011) in addition to being subsequently identified as a high potential spawning location (Lacho, 2013). Except at the confluence, single receivers were placed upstream of each site's riffles, with downstream receivers placed in a rectangular pattern near the riffles. Sync tags, which allow for the determination of triangulated tag positions, were mounted on selected receivers in each array. Final fish positioning was determined by triangulation, and resulting data filtered to retain records with reliable horizontal position error (HPE) values (HPE <15). Distance from each position point was measured to two polylines (left and right, facing downstream) at the extreme edges of polygons including both 2013 and 2014 substrate data (ESRI® ArcMap™, 1999-2010).

Spearman's rho (r_s) values were calculated for each receiver sync tag pair to assess the relationship between daily flow rates and daily averaged sync tag detections to determine if high flow rates diminished receiver detection capability (Appendix S2). Though peak flow levels rose to 1,460 m^3/s (Oldman River at the Mouth, 05AG006 station) and 3,320 m^3/s (Bow River at the Mouth, 05BN012 station), peak flow apex level was 398 m^3/s among acceptable HPE position values (HPE <15). Each sync tag reception/flow rate correlation pair was tested for significance using Bonferroni adjusted alpha levels of 0.004 per test (original p 0.05; 12 sync tag series assessed) (Appendix S2, Appendix S3). Results indicated that within HPE-validated flow levels, no detectable relationship could be ascertained for flow rate and detection efficiency; e.g., flow rate did not have a detectable negative impact on detection efficiency at flows less than 398 m^3/s. Changes in Lake Sturgeon behavior were calculated by creating a chronological polyline for each individual and calculating geometry for the polyline within ArcGIS. A buffered spatial join was performed to link each position point to daily flow rate data obtained from the nearest of two Alberta Environment monitoring stations nearest the study site (05AG006, 05BN012).

2.3 Results

2.3.1 Changes in Lake Sturgeon Habitat

Following the flood, large particle substrate area increased and fine particle substrate area decreased (Figure 2-1). A significant main effect was identified for overall substrate change, $F_{1,6} = 4.789$, $F_{\text{crit}} = 3.259$, $p = 0.014$, indicating fluvial substrate composition change occurred. The interaction between year and substrate was significant, $F_{1,6} = 5.571$, $F_{\text{crit}} = 3.259$, $p = 0.008$. Total mean area of larger-grain (gravel) substrate increased by 256% between 2013 (pre-peak flow) and 2014 (post-peak flow), while total fine-grain (silt-dominated) substrate area declined by 53%. There was a change in the mean area of gravel- and larger-substrate, which increased by 31,259 m^2, with mean area of interpolated gravel- and larger-substrate rising from 19,983 m^2 (2013) to 51,242 m^2 (2014) (t(6) = -6.29, SE = 4970, N = 7), (two-tail $p < 0.001$), providing evidence that high flow rates in 2013 and 2014 exposed larger particle fluvial substrate. A 95% C.I. about mean larger-particle substrate change was 19,098 to 43,419. Overall, there was a decrease in silt-dominated substrate mean area, which decreased from 28,949 m^2 (2013) to 13,575 m^2 (2014) (t(6) = 4.70, SE = 3271, N=7), two-tail $p = 0.003$), indicating that high flows tended to remove fine-grain substrate material, leaving larger-particle substrate material exposed. A 95% C.I. about mean fine-grain substrate change was -23,378 to -7,369. There was no detectable change in sand-dominated substrate. Mean area of sand-dominated substrate was reduced from 50,746 m^2 (2013) to 39,368 m^2 (2014) (t(6) = 1.02, SE = 11,117, N=7), (two-tail $p = 0.345$), C.I. (-38,580, 15,822)).

A significant correlation was identified when comparing habitat complexity and peak flow. Complexity as defined by patch density, (e.g. the number of identifiable contiguous, discrete substrate polygons of each substrate type per 100 hectares (Figure 2-3B), increased in

2014 relative to 2013. Following the flood, patch density increased from 183 mean patches per 100 ha (pre-peak 2013) to 256 mean patches per 100 ha (post-peak 2014) (M = 73.21, t(6) = -2.20, SE = 31, N = 21), indicating a measureable overall increase in complexity (two-tail *p* = 0.027), suggesting that the removal of silt exposed varying patterns of more complex and substantive underlying rocky substrate.

2.3.2 Changes in Lake Sturgeon Behavior

Lake Sturgeon showed a significant movement toward areas near the shore during the flood. Increases in flow rate showed a significant negative relationship to mean positional distance from shore (r = -0.654, $p < 0.001$, n = 45) implying that Lake Sturgeon move out of the main river channel to areas closer to the river's edge during periods of high flow (Figure 2-2). HPE-validated positions were recorded for flows ranging from 45.6 to 398 m^3/s, and locations ranged from 2.3 m (near) to 50.7 (far) from shore, with a 21.6 m mean positional distance from shore. Average position at minimum flow was 35.5 m from shore, at maximum flow, 2.93 m. The most frequent distance from shore (mode) was 16 m, which occurred 61 times, in flows ranging from 120 to 283 m^3/s.

2.4 Discussion

Large scale disturbance events, such as the extreme flood evaluated here, are expected to increase in many parts of the globe due to climate change (Andrishak and Hicks, 2008; Tahir *et al.*, 2011). Slight changes in temperature and precipitation have been correlated to dramatic changes in flood magnitude and frequency (Knox, 1993), and intensified precipitation and subsequent flooding are predicted as air temperatures rise (Knox, 1993; Bruce *et al.*, 1999; Fisher *et al.*, 2010; Fisher *et al.*, 2012). Glacier- and snowpack-fed rivers, such as those in the present study, are more acutely affected by climate change, increasing likelihood of flooding (Moore *et al.*, 2009; Fisher *et al.*, 2010; Tahir *et al.*, 2011). Given the increased frequency and magnitude of recent and predicted floods, understanding the impact on habitat and species-specific behavior is paramount for maintaining aquatic biodiversity.

Although extreme flood events may be costly to human life and infrastructure, they may be ecologically beneficial to some freshwater organisms (Naiman *et al*., 2008), particularly native, long-lived species such as Lake Sturgeon, that have adapted to large rivers with erratic flows successfully enough that a sufficient number of the species reach spawning age. The extreme flooding in Alberta in 2013 provided evidence of a positive disturbance event. Post-flood, there was an increase in the heterogeneity of potential spawning habitat of Lake Sturgeon. This can contribute to riverine biodiversity, especially when such heterogeneity is stimulated by disturbance (Ward, 1998). For example, macrobiotic communities have been shown to benefit from temporally irregular disturbance (Resh *et al*., 1988) as it results in increased species richness (Reice, 1985), with the greatest increases in macrobiotic densities occurring in the most afflicted disturbance zones (Snyder and Johnson, 2006), conferring the greatest increased resource benefit to the highest impact locations. Changes to overall riverine morphology resulting from disturbance-related increased heterogeneity may therefore enhance long-term resource availability for fish.

Lake Sturgeon may be well-adapted for tolerating extreme flood events. Southern Alberta experienced a period of deglaciation beginning 11,500 years ago, and ending 10,000 years ago (Wilson, 1996; Beaudoin and Oetelaar, 2003), post-dating the establishment of Lake Sturgeon populations in Alberta 18,000 years ago (Mandrak and Crossman, 1992; Guenette *et al*., 1993). The retreat of valley glaciers rendered marginal ice deposits unstable, resulting in large volumes of water and coarse sediment from runoff (Beaudoin and Oetelaar, 2003). Correlations between high flow rates and increased quality and quantity of sturgeon spawning habitat have been documented (Parsley and Beckman, 1994). Scouring offers sturgeon the "clean, (not silted) – rock, limestone or granite [substrate], 10–50 cm in diameter, with extensive clean interstitial spaces" (Bruch and Binkowski, 2002), they prefer, presumably because this substrate type offers the best chance of egg survival.

Extreme flood events can produce large changes in stream geomorphic features. For example, we show a scouring effect that can alter aquatic substrate, exposing and increasing larger-grain substrate types in the areas used for spawning. Increased substrate grain size and increased heterogeneity result from removal of fine-particle substrate material. Variations in refugia accommodate a broader range of species, enhancing overall ecosystem resilience, particularly where large-grain substrate is present (Doledec and Statzner, 1994; Townsend *et al*., 1997). Elevated heterogeneity offers velocity microrefugia.

Assessing species-specific behavior during an extreme flood event is rare. An overview of the few existing fine-scale fish movement studies surrounding flood events indicates variable, species-related responses. Radio-tagged Giant Kokopu (*Galaxias argenteus*) ceased all downstream movement and increased upstream movement during periods of flooding, and engaged in refuge-seeking behavior by means of relocation or micromovement (David and Closs, 2002). A study of Formosan landlocked salmon (*Oncorhynchus masou formosanus*) found that behaviors during floods did not differ from behaviors at normal water levels (Makiguchi *et al*., 2009). The ability of sturgeon to recognize and occupy optimal-velocity positions within the water channel has been shown elsewhere (Hurley *et al*., 1987; Kempinger, 1996; Curtis *et al*., 1997; Adams *et al*., 1999); however, ours is the first to demonstrate this behavior in situ under extreme flood conditions. Our results demonstrate that Lake Sturgeon show adaptive responses during an extreme flood event by avoiding the main channel and occupying optimal-velocity positions. Given the highly stochastic nature of extreme flood events, the ability to document Lake Sturgeon behavior and habitat changes during this extreme flood event was rare, and is useful in explaining Lake Sturgeon's ability to adapt to changing habitat conditions.

2.5 Figures

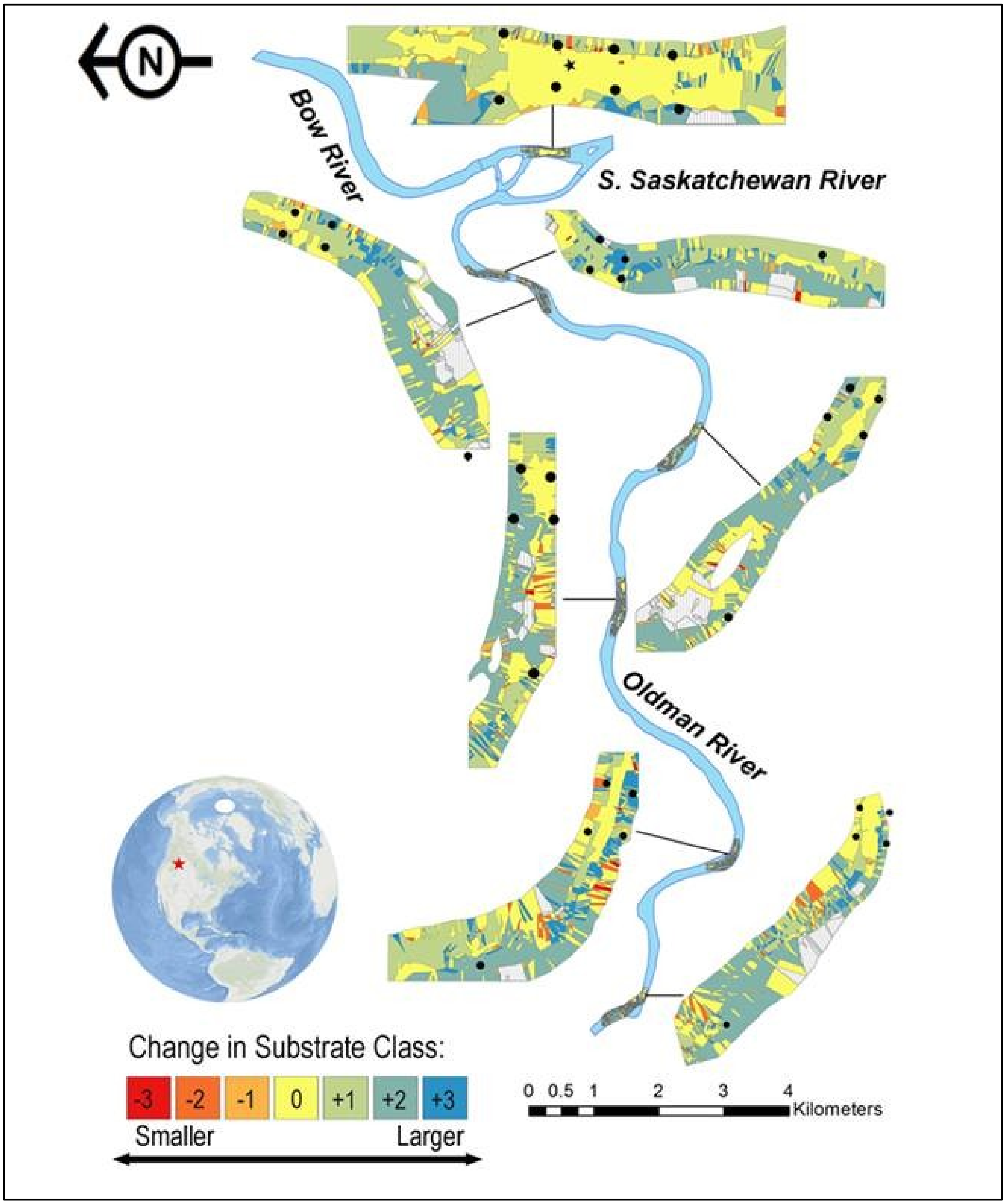


Figure 2-1. Location of Lake Sturgeon (*Acipenser fulvescens*) study in the Oldman and South Saskatchewan rivers in southern Alberta, Canada (bottom left). Maps show change in spawning substrate class from 2013 to 2014 following a record peak flow event in 2013. Legend (bottom left) shows change analysis results (-3: gravel to silt, -2: gravel to sand, -1: sand to silt, 0: no change, +1: silt to sand, +2: sand to gravel, +3 silt to gravel). VEMCO VR2W receivers are indicated by black circles; and reference tag by a black star.

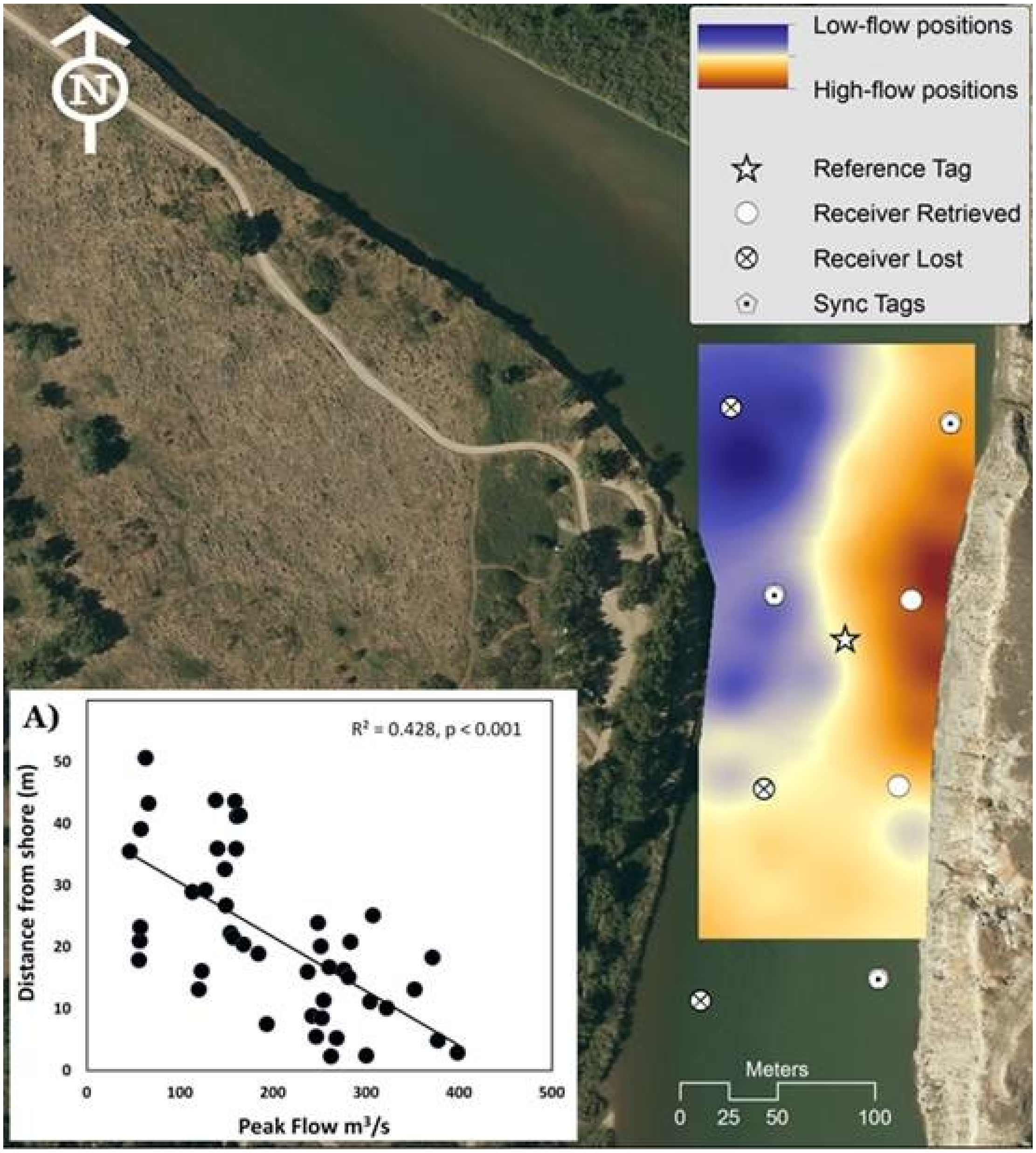


Figure 2-2. Grand Forks triangulated positions. Shown inset (A) are daily aggregated mean individual distance from shore by individual compared to daily peak flow rate. Lake Sturgeon showed a significant negative relationship to mean positional distance from shore (inset A).

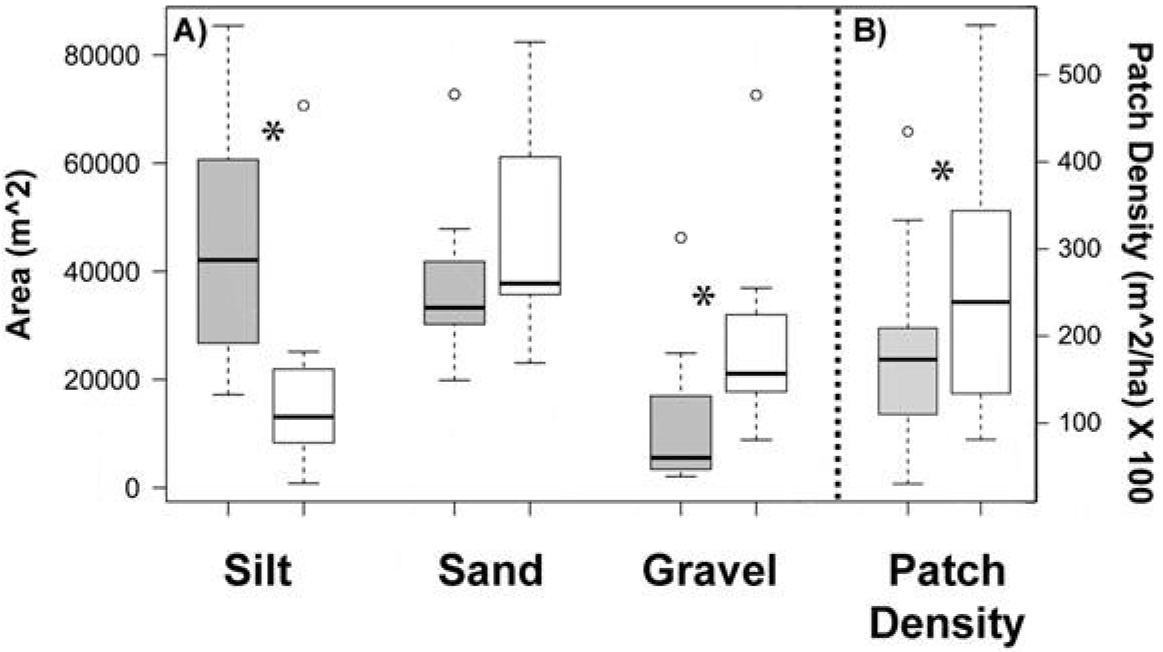
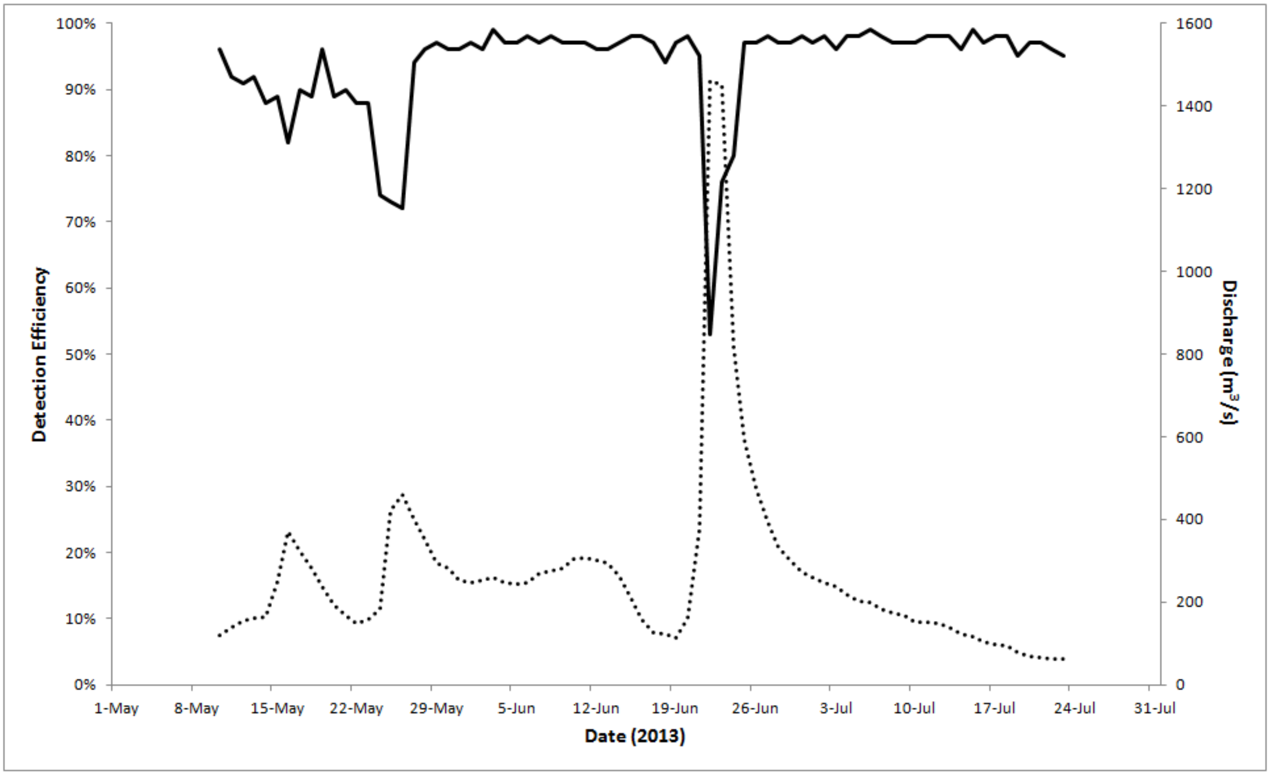


Figure 2-3. Change in substrate and complexity (patch density). Note: * $p < 0.05$ indicates significant change occurring between 2013 (gray bars) and 2014 (white bars).

Appendix 2-1. Peak discharge rates 1982-2014. At the time of our study, peak flow rate (m^3/s) was the highest ever recorded on the Bow River, Alberta across the collection period from 1982-2014. Also shown are single-day increases in flow, or pulses (m^3/s).

Peak Flow (m^3/s)	Date (mm/dd/yyyy)	Pulse (m^3/s)
1,470	04/09/2014	837
3,320	06/23/2013	1,850
841	06/27/2012	27
1,100	05/29/2011	477
431	06/20/2010	41
196	04/13/2009	57
875	05/27/2008	245
489	06/09/2007	26
778	06/18/2006	118
1,530	06/20/2005	728
265	07/10/2004	11
269	06/05/2003	18
535	06/12/2002	151
203	06/08/2001	37
131	04/02/2000	1
405	07/17/1999	104
684	06/22/1998	174
375	06/03/1997	36
319	06/11/1996	13
1,420	06/09/1995	781
486	06/09/1994	265
477	07/15/1993	83
627	06/17/1992	145
457	07/04/1991	6
817	06/05/1990	25
209	06/19/1989	33
220	06/12/1988	21
163	09/16/1987	5
415	06/02/1986	97
325	09/16/1985	90
159	07/05/1984	21
184	06/02/1983	99
301	07/02/1982	20

Appendix 2-2. Percent detection as assessed by sync tag transmissions received 5 by immediately adjacent receivers (%). Solid line represents detection efficiency (primary y-axis), dotted line discharge (secondary y-axis). Data not limited to flow rates where HPE-validated positions were identified.



Appendix 2-3. Comparison of sync tag transmission percent detections to peak flow rates (m^3/s). No relationship between flow rate and detections could be identified using Bonferroni significance variable (0.004). Positional distance from shore was assessed for all arrays, though an example map was provided for only the most active array (Grand Forks).

Sync Tag	Receiver	Position	RKM	Pearson's rho	*p*
65011	VR2W-119736	1DL	2.5	0.37	0.01
65137	VR2W-119732	1DR	2.5	0.05	0.77
65136	VR2W-119740	1UR	2.6	-0.12	0.43
65129	VR2W-110811	2UL	3.4	-0.19	0.24
65133	VR2W-119735	2UR	3.4	0.18	0.25
65020	VR2W-113001	5UL	15.7	0.08	0.62
65018	VR2W-100379	5UR	15.7	0.29	0.05
65022	VR2W-100381	6DL	18.8	-0.12	0.47
65023	VR2W-108963	6DR	18.8	0.18	0.26
65021	VR2W-109232	6UL	18.9	0.14	0.39
65019	VR2W-109236	6UR	18.9	0.28	0.07
65128	VR2W-110813	ForksL4	-0.3	0.29	0.06

Note: *p < 0. 004. No significant correlations found.

Chapter Three: **Fish under ice: Lake Sturgeon *(Acipenser fulvescens)* show highly restricted movement and habitat in winter**

ABSTRACT

This study represents the first fine-scale acoustic telemetry analysis of overwintering behavior and habitat selection for a Lake Sturgeon population occupying fluvial winter habitat. Fine-scale movement of adult and juvenile Lake Sturgeon were tracked using acoustic telemetry in a 1.5 kilometer reach of the South Saskatchewan River between October 22, 2013 and April 29, 2014. Period-segmented movement rates, depth selection, aggregation behavior and preferential overwintering habitat selection by adult and juvenile Lake Sturgeon were evaluated for a total of 26 (23 adults and 3 juveniles) individuals detected within the study area. Environmental parameters included depth, depth standard deviation (rugosity), bottom velocity, bottom velocity standard deviation, and substrate type (silt, sand, and gravel or larger substrate). Boosted regression tree (BRT) analyses were performed on period-aggregated core (50th percentile positions) and range (95th percentile positions) habitat variables derived from a 10 X 10 meter gridded map, reflecting receiver detection range. Movement rates paralleled temperature variation, becoming highly restricted during periods of deepest cold. Increased aggregation was also noted for these periods. The deepest habitat positions occurred during ice formation and breakup, ice-on period. The most predictive variables sturgeons used to identify preferred habitat included deep locations providing refuge and low bottom-velocity regions providing energy conservation during station-holding. Overwintering movement was minimal. Since Lake Sturgeon display site fidelity and aggregation behaviors independent of resource availability, winter habitat may be the most limiting critical habitat. While spawning habitat is crucial to ensuring successful recruitment, these data suggest that a substantial percentage of spawning adults spend the greater part of the year at their overwintering location, making this habitat potentially more critical to the survival of the population as a whole than any other habitat. If winter habitat is degraded or otherwise compromised, it could hinder species recovery, and should be considered critical habitat, receiving appropriate protection.

3.1 Preamble

In J. D. Salinger's *A Catcher in the Rye*, Holden Caulfield asks a deceptively simple question: "What do they do, the fish and all, when that whole little lake's a solid block of ice, people skating on it and all?" Holden receives the modern equivalent of a myth as his answer: Fish continue to live in the ice, frozen in place, and take in nutrition through their pores because Mother Nature takes care of them. With this absurd response, Salinger reveals much about our mid-century lack of knowledge about freshwater fish behaviors during periods when their movements and habitat choices are literally obscured (by ice) from direct observation. Since the book's release over a half century ago, fish overwintering behavior remains largely enigmatic.

3.2 Introduction

Individuals employ movement behaviors to secure acceptable physical and biological conditions in their environments and evade adverse conditions. Movement patterns among fishes, given the numerous and disparate spatial environments available to them, vary extensively (Albanese *et al*., 2004), and provide insight into species-specific survival and reproductive strategies (Kahler *et al*., 2001), and physiological limitations.

Understanding seasonal movement is important because fluctuating interannual environments drive migration behaviors and provide evidence of acceptable habitat. All migratory fish, including Lake Sturgeon (*Acipenser fulvescens*), exhibit seasonal movement toward acceptable spawning, feeding, and overwintering locations (Auer, 1996; McKinley *et al*., 1998; Linnansaari *et al*., 2009; Thomas *et al*., 2014). Lake Sturgeon show strong site-fidelity (Lyons and Kempinger, 1992; Auer, 1996). Habitat quality and resource availability at key seasonal stages affects recruitment dynamics, population density and age structure. Seasonal movement behaviors among individual Lake Sturgeon are more complex since migration patterns vary widely (Rusak and Mosindy, 1997; Auer, 1999; Smith and King, 2005; Gerig *et al*., 2011; Lacho, 2013), and are further complicated by non-age related spawning periodicity that varies among individuals (Auer, 1996; Forsythe *et al*., 2012), and idiosyncratic migration ranges (Forsythe *et al*., 2012; Wishingrad *et al*., 2014). Seasonal migration in these large-bodied, highly migratory fish can be particularly revealing, since these fish choose habitat from hundreds of kilometers of available habitat; in this population, over a thousand river kilometers are available as potential habitat (Lacho, 2013). Critical Lake Sturgeon core residency areas include overwintering sites as well as pre- and post-spawning sites (Auer, 1996), so understanding seasonal destinations provides insight regarding habitat selection choices. Recent research has shown that seasonal movement can be highly influenced by both body size and water body size (Woolnough *et al*., 2009), as well as sun angle, water temperature, and water flow rate (Lallaman *et al*., 2008; Forsythe *et al*., 2012). With an estimated mortality rate of 20% from harvest alone in the South Saskatchewan River population (Earle, 2002), this relatively small reach used by spawning-age individuals for the better part of a year meets the definition of critical habitat under Canada's Species at Risk Act. Identifying habitat required by this species for survival and ensuring the preservation of this habitat, and understanding seasonal movement and the factors driving them is vital to ensuring the successful conservation of this species.

For many temperate freshwater species, overwinter movement and habitat use remains as a large knowledge gap. Few studies are available on overwintering movement behavior and habitat selection for freshwater fishes in general (Hurst, 2007), though the few that have been performed highlight the grave challenges of the overwintering phase of a fish's life, including acute thermal stress, starvation, predation, hypoxia and physical injury from ice (Hubbs and Trautman, 1935; Magnuson *et al*., 1985; Cunjak, 1988; Hurst, 2007; Linnansaari *et al*., 2009). Despite these stressors, far more research on fish movement behavior and habitat selection has been performed during non-winter periods (Rusak and Mosindy, 1997; Crossman *et al*., 2009; Linnansaari *et al*., 2009), including telemetry studies, which have primarily conducted in spring and summer (Hay-Chmielewski, 1987; Holtgren and Auer, 2004; Smith and King, 2005; Crossman *et al*., 2009).

Lake Sturgeon is an important species in terms of conservation status and scientific research. As a large, bottom-feeding fish, the species has shown importance as environmental indicator species (Casselman *et al*., 1999; Lagutov, 2008). Its large body size requires commensurately extensive, unfragmented, undegraded habitat, though eggs, fry, and young-of-the-year (YOY) are vulnerable to predation (Kynard *et al*., 2005; Bruch *et al*., 2006; Alberta Lake Sturgeon Recovery Team, 2011). Their return to the Detroit River signaled what some referred to as "one of the most remarkable ecological recoveries in North America" (Hartig *et al*., 2007; Hartig *et al*., 2009; Hartig, 2014). As a relict species (sturgeon make up approximately 50% of extant species of the plesiomorphic Chondrostei infraclass), Acipenseriformes present a compelling outgroup for molecular phylogenetics studies, providing insight into genetic variations in comparison to other fishes with Chondrosteidae roots, including fishes in the Actinopterygian and Osteichthyan classes (Grande and Bemis, 1991). As a species targeted for conservation, Lake Sturgeon have been identified as a globally and nationally vulnerable species (G3, N3) (NatureServe, 2013) believed to be at risk throughout their range (Peterson *et al*., 2007). Rehabilitation efforts have been effective in restoring populations in some regions and the species designation has been downgraded at a global level to Least Concern (IUCN, 2015). Federally, the species is under consideration for addition to Schedule 1 of the Species at Risk Act (Alberta Lake Sturgeon Recovery Team, 2011; Pepper, 2012; COSEWIC, 2014). In December 2007, the DU2 Lake Sturgeon population was listed as "Threatened" under the Wildlife Act (Alberta Lake Sturgeon Recovery Team, 2011).

Only a handful of studies have been conducted on overwintering behaviors in Lake Sturgeon (Rusak and Mosindy, 1997; Huusko *et al*., 2007; Trested *et al*., 2011; Ghilarducci and Reeve, 2012). This study represents the first fine-scale acoustic telemetry analysis of overwintering behavior of Lake Sturgeon in fluvial habitat. Objectives include, i) identifying Lake Sturgeon overwintering movement patterns and habitat use, ii) identifying temporal variations in movement rate, depth selection, and aggregation propensity, specifically focusing on diurnal (day/night), monthly, and ice-on/off time periods, iii) comparing juvenile and adult movement rates for the overall period, and, iv) collective habitat selection for diurnal (day/night), monthly, ice-on/off time periods, and the entire study period.

3.3 Materials and Methods

3.3.1 Study site

This study took place in the South Saskatchewan River in a ~1.5 kilometer reach of river, approximately 85 river kilometers downstream of Medicine Hat (Figure 3-1). This location was chosen as it was previous identified as overwintering habitat for Lake Sturgeon (Lacho, 2013; Carr *et al*., 2015). This reach of the river had low bottom velocities and comparatively greater pool depths (> 5 m) consistent with overwintering habitat variables identified in other studies (Hay-Chmielewski, 1987; Rusak and Mosindy, 1997; Adams *et al*., 2006). A systematic grid array was deployed on October 21-22, 2013 including 36 acoustic receivers placed within 100 meters of each other, two reference position transmitters (ref tags) and a test tag receiver. Of these, 31 receivers were retrieved on April 29-30, 2014.

3.3.2 Acoustic tagging and study population

A total of 123 Lake Sturgeon (626-1601 mm) were surgically implanted with Vemco V16 coded acoustic transmitters, including 34 individuals tagged between 2010-08-15 and 2010-10-01, and 89 individuals tagged between 2011-05-03 and 2011-08-24. Implanted transmitters emitted sonic pulses at, on average, a 2 minute interval. Tag transmissions were detectable typically 500-1900 meters from the VEMCO VR2W receivers (Lacho, 2013; VEMCO, 2015). The transmitter code, date, and time of the pulse were received by the hydrophone, transferred to the ID detector, and stored in memory by the data-logger. Data were retrieved on April 29 and 30, 2014, and processed for positioning by VEMCO. Greater than 50% of all position values showed error rates lower than 13.8; 75% of animal detection horizontal position error (HPE) values were lower than 18.9. Data were filtered to retain records with reliable HPE values lower than 15 (HPE <15) (Espinoza *et al*., 2011; VEMCO, 2015). After excluding individuals not present throughout the study, final HPE values ranged from 10.4 to 14.9, with minimal temporal variations across the study period (mean = 12.70 ± 1.8).

3.3.3 Receiver stations

VEMCO™ VR2W (69 kHz) omnidirectional hydrophones were positioned ~ 40 cm above the river bottom, to depths ranging from 1-5.3 meters. To correct for clock drift and to assess detection efficiency, each receiver was moored along with a synchronization tag (sync tag). Total sync tag detections per receiver ranged from 255,670 (receiver St01) to 852,175 (receiver St28); transmissions detected ranged from 99,154 detections (sync tag S36) to 309,750 detections (sync tag S11), with a mean of 190,181 transmissions detected (Figure 3-2). Sync tag transmissions were detected by an average of 9 stations, with 90.6% of sync tag transmissions detected by 3 or more receivers.

3.3.4 Habitat variables

3.3.4.1 Substrate and bathymetry

Bathymetry and substrate data were collected on October 17, 2013 under conditions of 170 m^3/s total flow (Figure 3-3, Appendix 3-1) (Environment Canada, 2015). Data were collected using a single beam 200 kHz transducer MX Aquatic Habitat Echosounder (BioSonics, Inc., Seattle, Washington, U.S.A.) with a nine-degree beam angle emitting 5.0 pulses per second for 0.4 millisecond per pulse. Each transducer pulse travels through water at an approximate speed of 1,500 meters per second. When a pulse reaches the river bottom or another solid object, the reflected acoustic pulse is received by the transducer. Signals exceeding a threshold level are identified on the echogram, and their travel time is used to calculate range (distance from the transducer). Hard bottom types such as rock or gravel produce a sharp, high-amplitude echoes, while soft bottom substrate types such as silt produce an elongated, lower-amplitude echo (Burczynski, 2002). Data were validated at 19 snorkeled sites (Figure 3-5, Table 3-2).

Raw data were processed using Visual Habitat software (BioSonics Inc., 2013). Transects with no clear and visible bottom edge were removed from the dataset. Bottom detection analysis was performed using the bottom detection tool set at recommended with manual corrections where necessary.

A feature extraction was performed with a first part bottom echo of single pulse length and a second-part bottom echo of pulse length X 3, with depth normalization enabled and a fractal dimension threshold of -60. To increase analytical sensitivity, energy filter width was decreased from the default value of 20 pings (averaged) to 5 pings (averaged). A three cluster classification using a fuzzy C-means clustering analysis was performed using Visual Habitat software (BioSonics Inc., 2013) to derive substrate classifications (Bezdek *et al*., 1984). The fuzzy clustering principal components analysis technique is an unsupervised machine learning algorithm that identifies patterns in unlabeled data, and is comparable to unsupervised classification methods used to categorize large-scale land-cover types (Foody and Cox, 1994; Zhang *et al*., 2014). Fuzzy cluster memberships using this technique correlated strongly with actual memberships identified independently (Foody and Cox, 1994; Zhang *et al*., 2014). Resulting data were loaded into ArcMap (ESRI® ArcMap™, 1999-2010) and interpolated for the entire study area via Euclidean allocation (Locker *et al*., 2010) and compared to substrate types identified by snorkeling (Table 3-2). Bottom elevation was measured directly by the echosounder and interpolated using Inverse Distance Weighting (IDW) interpolation (Gotway *et al*., 1996; Zimmerman *et al*., 1999) in ArcMap.

3.3.4.2 Bottom velocity

Bottom velocity data were acquired on April 29, 2014 under conditions of 265 m^3/s total flow (Figure 3-3, Appendix 3-1) (Environment Canada, 2015). Data were collected using a SonTek River Surveyor M9, a nine-beam Acoustic Doppler Current Profiler (ADCP) mounted on a hydroboard and towed from a nylon line attached to a ~2-3 meter dowel extending from the bow of a single-engine boat. The instrument acquires velocity profiles (pings) at a frequency of 1 Hz for depths between 0.2–30 m by means of two sets of four profiling beams (3.0 MHz and 1.0 MHz, respectively) and one depth-measuring vertical beam (0.5 MHz) (SonTek, 2014). Mean boat speed was 2.72 ± 1.6 km/hour. Of a series of 33 transects approximately 50 meters apart, 30 transects (Figure 3-4) presented data with a signal-to-noise ratio greater than 1. Transects with signal-to-noise ratios below this threshold were removed from the analysis. Data smoothing was performed by calculating a three-point moving average (Unal and Ozcakal, 2011) prior to interpolation in order to manage artifacts, particularly at edges, in the transect data. Resulting datapoints were mapped and a Kriging interpolation applied to these points to create a raster.

3.3.5 Movement rates, depth selection, and aggregation over time

A permuted analysis of variance (ANOVA) was used to assess temporal movement, depth selection, and aggregation patterns for all models. Permuted ANOVA techniques have been used in similar studies evaluating non-parametric data with unequal sample sizes, and are robust to assumptions of non-normality (Ruppert *et al*., 2013). Each permuted ANOVA used 999 permuations and was performed in R (Legendre and Legendre, 2012). A post hoc Tukey's HSD (honest significant difference) test (Tukey, 1949) was performed for analyses with multiple factors in order to identify significant differences.

3.3.5.1 Movement rates

Distances were measured between consecutive, error-corrected positions for each individual fish by creating discrete polylines from sequential individual positions (Figure 3-6 and Figure 3-7) within the water polygon using FishTracker (Laffan and Taylor, 2013). Distance traveled per segment (kilometers) was divided by date-time (days) as divisor to calculate movement rates as kilometers per day. A secondary calculation to confirm distance traveled (kilometers) was performed using great-circle distances between each consecutive position via the spherical law of cosines, a variation of the Haversine formula (Sinnott, 1984; Maling, 2013).

$$\mathrm{km} = \operatorname{acos}\big(\sin(\mathrm{lat1}) * \sin(\mathrm{lat2}) + \cos(\mathrm{lat1}) * \cos(\mathrm{lat2}).\cos(\mathrm{lng2} - \mathrm{lng1})\big) * \mathrm{R}$$

Where

km = distance (kilometers) between two points described in decimal latitude/longitude

lat1, lng1 = position 1

lat2, lng2 = position 2

R = 6371 km (earth's radius)

Permuted ANOVA were performed for four models: a) diel values for the entire study period, b) ice on and ice off periods, c) monthly periods, d) and juvenile/adult movement for the entire study period, using total daily kilometers traveled as the dependent variable for all models. Individuals not present during all periods assessed (e.g. – for monthly analysis, an individual not present in November, but present for the remaining months) were excluded from analysis.

3.3.5.2 Depth selection

Triangluated positions were intersected with the bathymetry raster using the isectpntrst tool within Geospatial Modelling Environment (GME) software (Beyer, 2012) and the resulting table exported for analysis.

Permuted ANOVAs were used to assess four models: a) diel values for the entire study period, b) ice on and ice off periods, c) monthly periods, d) and juvenile/adult depth selection for the entire study period, using daily average depth as the dependent variable for all models. Individuals not present during all periods assessed were excluded from analysis.

3.3.5.3 Aggregation

Two positional subsets were created for each fish active during all months of the study (n=20), one subset including all positions for a specific fish (target fish), and one subset for all non-target fish positions (conspecifics). Using daily intervals, the distance from each mean conspecific position to the mean target fish position was calculated using paired (target fish, all other fishes) XY coordinates (Figure 3-16). Fish were considered to be aggregating if the distance from conspecific to the target fish fell within the 10th percentile (200m) of all calculated distances. A count of the number of conspecifics within the 200 meter defined aggregation range was performed for each day to determine aggregation propensity (Figure 3-17). Resulting data were assessed using a permuted ANOVA with 999 permutations.

3.3.5.4 Determination of ice-cover periods

Water temperature data were collected from a HOBO datalogger (LGR S/N: 2408819, SEN S/N: 2408819) attached to a receiver located downstream of the overwintering site.

Temperatures were logged every hour. Mean daily values were used to determine when water temperatures did not rise above 0°C (November 11, 2013), and this date was designated the beginning of the ice-on period. The date after which water temperatures remained consistently above 0°C (April 10, 2014) was designated the end of the ice-on period.

3.3.6 Core and range habitat selection for five models

To avoid overweighting habitat variables arising from movement-related spatial collinearity, all positional data were aggregated and assigned to a series of 10 X 10 m grid cells, reflective of receiver range, prior to running a boosted regression analysis. A 10 X 10 m grid cell polygon layer was prepared in ArcMap (ESRI® ArcMap™, 1999-2010) to cover the study area, and habitat data were summarized for each cell using Geospatial Modelling Environment (GME) software (Beyer, 2012) using the isectpolyrst tool. Finished habitat datasets included seven variables: depth mean, depth standard deviation, bottom velocity mean, bottom velocity standard deviation, percent silt, percent sand, and percent gravel or larger substrate. GME software was also used to calculate 50% (core) and 95% (range) volume contour isopleths from composite positional data for five models, including, a) diel values for the entire study period, b) ice on and ice off periods, c) monthly periods, d) juvenile/adult habitat selection for the entire study period, and e) overall habitat selection for the entire study period. These isopleths were imported to ArcMap, and each model merged with related summary habitat data using the select by layer tool. Data were exported as comma-delimited files to be assessed in R.

A boosted regression tree (BRT) analysis (Elith *et al*., 2008) was performed on resulting datasets to assess habitat selection for the five models with tree complexity = 5, bag fraction = 0.5, and learning rate was adjusted to achieve the optimal number of trees (between 1,000 and 2,000 trees). To determine the selection direction for each variable, regression trees based on recursive partitioning (CART) were generated within R for each period using a random sampling of 75% of the dataset to train and the remainder to test. CART models have been used in previous studies to identify top contributor variables and patterns (Ruppert *et al*., 2009). Variable selection direction was based on test data pruned to a complexity parameter of 0.02.

3.4 Results

3.4.1 Detections

A total of 86 Lake Sturgeon were detected in the Oldman, Bow, Red Deer and South Saskatchewan rivers between October 21, 2013 and April 30, 2014 (Table 3-3). Of these, 26 individuals were detected with more than one HPE-validated triangulated positions (23 adults and 3 juveniles); 20 of which were present during all period segments. Receivers logged 11,326,072 fine-scale animal tag detections over the study period, 67.7% of these transmissions were acquired by > 3 receivers, with a mean of 6.6 receivers detecting each animal tag transmission. Overwinter residents with sufficient HPE-validated positions for analysis represented 30.2% of all tagged sturgeon and 40.4% of the adult population from ~1,100 kilometers of available riverine habitat (Table 3-3). Of individuals overwintering at South Saskatchewan River winter study site, 88% were classified as adults, compared to the overall population detected elsewhere during that period, 65% of which were adults (Figure 3-11).

3.4.2 Movement rates, depth selection, and aggregation over time

3.4.2.1 Movement rates

Total daily movement patterns averaged for the cohort (Figure 3-12) generally corresponded with temperature changes. Ice-on movement rates were low and variable both for the cohort and among individuals. Permuted ANOVA results revealed significantly greater movement among the cohort ($p < 0.001$) during ice-free periods (mean = 0.89 km/day) when compared to ice-cover periods (0.19 km/day) Movement rates increased significantly ($p < 0.001$) in April (mean = 1.00 km/day) compared to all other months (monthly mean movement for November = 0.30 km/day, December = 0.17 km/day, January = 0.16 km/day, February = 0.19 km/day, March = 0.28 km/day). No significant differences were noted when comparing day (mean = 0.19 km/day between dawn and dusk) to night movement (mean = 0.21 km/day between dusk and dawn), ($p = 0.579$) or between adult overall movement (mean = 0.30 km/day) and juveniles (mean = 0.33 km/day), ($p = 0.519$). See Figure 3-13 and Table 3-4 for movement rate analysis summaries.

3.4.2.2 Depth selection

Lake Sturgeon occupied locations with greater depth within the study area during periods of ice formation and ice break-up (Figure 3-14). Permuted ANOVAs identified the most significant positional depth variation among monthly periods, with the deepest mean daily positions occurring in November (mean = -3.67 m), the shallowest in April (mean = -2.77 m), ($p < 0.001$), with positions at slightly deeper locations in December (mean = -3.33 m), and relatively equivalent depths in the remaining months (January mean = -2.93 m, February = -2.93 m, March = -3.01 m). Less pronounced differences in depth selection were found between overall ice on periods (mean = -3.17 m) and ice off periods (mean = -2.90 m), (p=0.003). No difference was found for depth selection when comparing day (mean = -3.16 m) with night (mean = -3.10 m) depth values (p=0.155) or juvenile depth selection (mean = -3.12 m) in comparison to adult depth selection (mean = -3.01 m) across the study period (p =0.106). A confounding factor may include an unbalanced dataset; 88% of individuals overwintering at South Saskatchewan River winter study site were classified as adults, compared to the overall population detected within the greater study area for that period, of which, 65% were adults (Figure 3-11), and insufficient power among juveniles (n=3) may have influenced results. See Figure 3-15 and Table 3-5 for depth position analysis summaries.

3.4.2.3 Aggregation

Aggregation behavior, defined as the number of conspecifics located within 200 meters of any single individual, increased among Lake Sturgeon during winter months. Though mean inter-individual distances did not reveal an overall trend, minimum mean distances among individuals were notably small during periods of ice formation and breakup (Figure 3-16). Permuted ANOVAs identified significant differences in aggregation behavior when comparing monthly periods ($p < 0.001$), with the greatest daily mean aggregation occurring in December (4.07 conspecifics within 200 meters from target fish, indicating a grouping of five fish). November showed the second highest mean aggregation (3.52 close conspecifics/day), followed by January and February (3.28 close conspecifics/day), diminishing thereafter (March = 1.93, and April = 1.38 close conspecifics/day). Juveniles tended to aggregate with conspecifics (4.10

close conspecifics/day) to a greater degree than did adults (2.60 close conspecifics/day), ($p < 0.001$). The cohort as a whole aggregated more during ice cover periods (3.03 close conspecifics/day) than during ice-free periods (2.01 close conspecifics/day), ($p = 0.003$). Aggregation propensity did not vary when comparing day (2.89 close conspecifics/day) with night (2.88 close conspecifics/day) across the study period ($p = 0.962$) (Table 3-6).

3.4.3 Core and range habitat selection for five models

Overall, Lake Sturgeon overwintering in South Saskatchewan River winter study site selected deep areas with low, constant bottom velocities (core habitat) and areas with greater slope variation (range habitat) (Figure 3-18, Figure 3-19). BRT analyses found depth and bottom velocities to be the most influential environmental variables for both core (50 percentile) and range (95 percentile) habitat extents for all temporal segments assessed. Depth and bottom velocity, in different arrangements, account for all primary and secondary predictive variables, with rugosity the leading secondary predictive indicator for March core positions (Appendix 3-3, Appendix 3-4). Depth was the predominant predictive variable for core areas before ice break-up, bottom velocity the most predictive for core habitat during April and ice-free periods. Substrate types were the least predictive core habitat variables. Range percentiles showed depth as the top predictive habitat variable for November through February, bottom velocity as the top predictive variable elsewhere (Appendix 3-3). Secondary predictors for range percentiles reversed these variables.

3.4.3.1 Core habitat selection

Core habitat variables indicate Lake Sturgeon occupied deep (35.6% – 57.4% relative contribution, mean = 42.75% ± 7.73%) and low bottom velocity areas (30.6% – 39.2% relative contribution, mean = 35.53% ± 4.44%) (Figure 3-18, Figure 3-19), with core presence positions occurring in locations at mean depths greater than 2.8 m ± 0.09 m and bottom velocities under 0.65 m/s ± 0.10 m/s (Table 3-7). Depth was the top predictive variable for core habitat in all period segments except April, Ice-Off, and overall periods, where bottom velocity contributed the highest predictive potential (Appendix 3-3). Depth was the second-most predictive core variable for periods where bottom velocity was the top predictive variable (27.1% – 28.7% relative contribution, mean = 27.6% ± 0.92%), and bottom velocity where depth was the top predictive variable (16.4% – 32.7% relative contribution, mean = 25.87% ± 5.57%), save for March core, where rugosity (depth standard deviation) was the secondary predictive variable (Figure 3-18, Figure 3-19, Appendix 3-4). Predictive differences between depth and bottom velocity as the two top and secondary predictive variables are confounded by the sizeable influence of multicollinearity (Table 3-9). Rugosity was a contributing factor in two core recursive partitioning models, core April and ice-off, where Lake Sturgeon preferred habitat with depth standard deviations greater than 0.13 m (Table 3-7).

3.4.3.2 Range habitat selection

For range habitat, depth and bottom velocity were the top predictive variables (Figure 3-18, Figure 3-19, Appendix 3-3), with bottom velocity providing the highest mean predictive capacity by a small margin (35.0% – 40.8% relative contribution, mean = 37.9% ± 1.76%) when compared to depth (29.7% – 45.1% relative contribution, mean = 37.8% ± 6.85%). Bottom velocity was the chief predictive habitat variable in all periods except November through February monthly segments. Range positions occurred in locations at mean depths greater than 2.82 m ± 0.13 m and bottom velocities lower than 0.55 m/s (Table 3-8). Where depth was most predictive in a given model, bottom velocity was the secondary variable; conversely, where bottom velocity was most predictive, depth was the secondary variable. Bottom velocity contributed 20.1% –24.6% to predictions, mean = 22.7% ± 2.11%, slightly more predictive than depth (19.0% – 27.9% relative contribution, mean = 21.5% ± 3.00%). Depth and bottom velocity were the sole secondary predictors of preferred range habitat.

Strong multicollinearity among predictor variables was an important confounding factor (Table 3-9). The impact of sandy substrate as a predictive variable was likely superseded by depth, with which it shares a 0.81 correlation. A 0.56 correlation between sandy substrate and bottom velocity variables may have also had an impact. Depth and bottom velocity variables were also strongly collinear with a 0.60 correlation.

3.5 Discussion

Lake Sturgeon are large, benthic fishes that inhabit large, perennial rivers where aquatic biota are diverse and plentiful (D'Ambrosio *et al*., 2014) and velocities low (Barth *et al*., 2009). Proximity to deep pool overwintering habitat (i.e., >1.5 m deep) (Hay-Chmielewski, 1987) has been identified as a primary factor in spawning site selection (Bruch and Binkowski, 2002). While scientific observations of Lake Sturgeon spawning behaviour have been documented since 1919 (Nevin, 1919; Bruch and Binkowski, 2002), their winter movement patterns and preferential use of microhabitat remain largely uninvestigated (Auer, 1996). Some studies have reported overwintering aggregation behaviors in sturgeon (Barth *et al*., 2009) that cannot be explained by resource availability alone (Nilo *et al*., 2006; Trested *et al*., 2011). Recent improvements in acoustic telemetry technology, specifically, VPS combined with numerous habitat assessment methods, allow for better understanding of Lake Sturgeon overwintering resource use. Refining our understanding of winter resource use is a crucial step in conservation and rehabilitation of this cohort of Lake Sturgeon and similar populations.

3.5.1 Movement rates, depth selection, and aggregation over time

This study presents the first fine-scale acoustic telemetry overwintering study of movement and habitat selection for a Lake Sturgeon cohort occupying solely fluvial habitat. Bathymetry analysis performed in a separate study indicates limited deep habitat for this study population, with ~5.7% of the river possessing depths greater than 3.5 meters (Table 3-10), implying that these sturgeon have selected this reach for its depth. Movement behaviors of 26 individuals (20-23 adults, 3 juveniles) in the South Saskatchewan River demonstrated sensitivity to seasonal cues and selection tendency toward for deep, low bottom velocity overwintering habitat. These large-bodied fish, too large to shelter in rocky interstitial spaces, seek habitat with sufficient depth to provide requisite cover, and sufficiently low bottom velocity to allow for energy conservation during station holding, findings in concurrence with previous research (Cunjak, 1996; Hughes *et al*., 2000; Sulak and Randall, 2002; Cech and Doroshov, 2004). In the present study, as temperatures decreased, cohort members moved less and aggregated more.

Winter dormancy and residence in deep pool areas within rivers have been described as life history traits common among most sturgeon species (Sulak *et al*., 2007), and may be adaptive behavioral responses to challenging seasonal conditions. In the current study's cold temperature environment, swimming may be impaired by slowed metabolic rates and by the added difficulty of movement under higher viscosity waters in cold temperature conditions as has been previously documented (Webb, 1975; Beamish, 1978; Fuiman and Batty, 1997). Localized reductions in dissolved oxygen arising from ice cover, fewer daylight hours, lower light intensity, reduced photosynthetic biomass, benthic decomposition, and aggregation proclivities have also been shown to reduce fish movement and influence small-scale habitat selection (Greenbank, 1945; Cooper and Washburn, 1949; Hasler *et al*., 2009).

Increased movement and dispersal activity on March 12-14 corresponds with a period of anomalous extreme heat following deep cold that resulted in snowmelt flooding throughout the province. Mean ambient air temperatures rose from -25.8°C on March 1, 2014 to 8.8°C on March 9, 2014, remaining above freezing and reaching another high of 7.6°C on March 12, 2014, returning to below freezing temperatures on March 20, 2014. Weather conditions during this period prompted the Alberta Environment and Sustainable Resource Development Department to issue an emergency alert on March 10, 2014 (Government of Alberta, 2014). The melt increased turbidity in upper reaches of the tributary Bow River to the degree that the treatment facility could not process water and a Boil Water Alert was issued on March 10, 2014 and remained in effect until March 14, 2014 (City of Lethbridge, 2014). A similar spike occurred in January, and was concurrent with sustained elevated air temperature. Both movement and aggregation patterns returned to previous levels after air temperatures fell below 0°C. Lake Sturgeon behaviors were not formally compared to air temperatures in this study, but these coincident observations suggest that these movement anomalies were related to periods of elevated air temperatures.

Results of this study provide evidence that this cohort of Lake Sturgeon exhibits limited winter movement and increased aggregation behaviors, a finding in alignment with observations of winter movement and aggregation patterns in other sturgeon species (Bemis and Kynard, 1997; Rusak and Mosindy, 1997; Kynard *et al*., 2000; Kynard *et al*., 2005; Ghilarducci and Reeve, 2012).

Overwintering movement rates did not vary significantly from day to night, augmenting previous research on this population that identified a significant diel response during non-winter months (Lacho, 2013). Conflicting results exist regarding diel movement patterns in sturgeon (Lacho, 2013), with some studies reporting no diel movement (Haynes and Gray, 1981; Moser and Ross, 1995) and some reporting strong diel movement (Parsley and Beckman, 1994; Kynard *et al*., 2005; Wrege *et al*., 2011). Even within a single study, sturgeon diel movement patterns shifted from strong diel orientation to none (Zhuang *et al*., 2002). In the current study, though absolute movement rates did not vary from day to night, near-significant affects were found when comparing day to night depth selection and aggregation behavior, indicating that the role of light is unclear. In this population, resident in a northern prairie river and subject to extreme cold, winter torpor may exert a stronger influence on movement behavior than diurnal pressures.

Juvenile and adult movement rates did not differ in the amount of and variation in movement patterns, though this may have resulted from lack of power given the limited number of juveniles (3) resident in the study area during the study period.

Temporal depth selection revealed a fairly consistent preference for deeper habitat during periods of ice formation and break-up, further indication of depth locations as refugia from flowing ice and debris. Depth selection analysis was limited to spatial selection of specific bathymetric locations; movement within the water column was not assessed. The triangulation method used provided a two-dimensional spatial location only, prohibiting analysis of diel vertical migration and depth selection by free swimming within the water column.

3.5.2 Core and range habitat selection for five models

Both depth and bottom velocity were important predictors of overwintering core habitat selection as determined by boosted regression techniques, dominating as the top and secondary predictive habitat variables for all core and range periods, corroborating the supposition that deep habitat provides a concealment refuge for these large-bodied fish, and low-velocity microhabitats provide velocity refugia, allowing for maximal resting-position energy conservation. Depth was the primary core habitat variable for all non-spring and overall positions. Where depth was the topmost habitat variable, in all but March core, bottom velocity was the secondary habitat variable.

Depth and bottom velocity were also the top variables for range habitat, with bottom velocity primary in all segments except November through December monthly periods, where depth was the top selector variable. Secondary habitat variables were the inverse, with depth replacing bottom velocity as primary and bottom velocity replacing depth. Relative contribution to predictive capability implies that both depth and bottom velocity are fundamental habitat conditions sought by Lake Sturgeon. Substrate type did not show a strong influence on habitat selection, though this does not necessarily contradict numerous studies reporting sandy substrate as a primary overwintering habitat variable (Rusak and Mosindy, 1997; Smith and King, 2005; Lacho, 2013). Strong multicollinearity between sandy substrate, depth and bottom velocity may have reduced sandy substrate's rank as a predictive variable.

3.5.3 Management implications

Of the 86 fish detected during the study period, 26 Lake Sturgeon individuals with 1,100 river kilometers of accessible habitat selected this 1.5 kilometer stretch of river for overwintering, 23 of them resident throughout the entire period (October 2013 through April 2014). To put this into perspective, 23 out of 86 (26%) of all detected sturgeon, including 20 out of 57 adults, or 35% of the entire tagged adult population, spent half the year in 0.14% of their available habitat. While spawning habitat is crucial to ensuring successful recruitment, these data suggest that a substantial percentage of spawning adults spend the greater part of the year at their overwintering location, making this habitat potentially more critical to the survival of the population as a whole than any other habitat. If winter habitat is degraded or otherwise compromised, it could hinder species recovery, and should be considered critical habitat, receiving appropriate protection. Overwintering movement is limited here as in other studies

(Hay-Chmielewski, 1987; Fortin *et al*., 1993; Rusak and Mosindy, 1997; Trested *et al*., 2011). A completely fluvial population, these individuals are further challenged by station-holding energy expenditures in comparison to lacustrine migratory populations of the same species (Fortin *et al*., 1993; Peake *et al*., 1997; Adams *et al*., 2003). Since sturgeon display site fidelity (Barth *et al*., 2011; Pledger *et al*., 2013; Thomas *et al*., 2014) and aggregation behaviors (Kynard *et al*., 2011) independent of resource availability (Nilo *et al*., 2006; Kynard *et al*., 2011; Trested *et al*., 2011), overwintering habitat creates a potential limiting factor that, if degraded or otherwise compromised, could critically hinder species recovery.

3.5.4 Conclusion

Analysis of fine-scale Lake Sturgeon movement and habitat selection during the overwintering period indicates that these large-bodied individuals find cover in deep-water habitat during the coldest months and seek velocity refugia in their range movements. They avoid injury from ice formation and ice breakup by moving to deepest habitat during periods of temperature fluctuation in winter and spring. They conserve energy during periods of cold temperatures by limiting their movements and inhabiting low bottom velocity habitat and aggregate with conspecifics as temperatures drop.

3.6 Tables

Table 3-1. Raw and adjusted total lengths for Lake Sturgeon entering the South Saskatchewan River winter study area in 2013-2014. Adjusted per Royer estimates of age-dependent growth rates for Lake Sturgeon in the Saskatchewan River delta (Royer *et al*., 1968).

ID	Growth/ year (mm)	Total Growth (mm)	Raw TL (mm)	Adjusted TL (mm)
63336	53	106	717	823
288	53	106	747	853
318	53	106	891	997
48572	53	106	1060	1166
48589	53	106	1180	1286
48562	53	106	1157	1263
48616	53	106	1166	1272
48575	53	106	1185	1291
303	13	26	1223	1249
48617	13	26	1296	1322
48570	13	26	1313	1339
48592	13	26	1311	1337
48563	13	26	1357	1383
342	13	26	1368	1394
48613	13	26	1364	1390
324	13	26	1342	1368
346	13	26	1386	1412
48576	13	26	1397	1423
48569	13	26	1407	1433
48567	13	26	1402	1428
48574	13	26	1432	1458
316	13	26	1489	1515
48614	8	16	1470	1486
328	8	16	1540	1556
48565	8	16	1545	1561
48566	8	16	1601	1617

Table 3-2. Snorkeled validation points used for substrate analysis. Interpolation/validation conflicts highlighted.

Index	Ping #	Latitude	Longitude	Substrates	Interpolated Substrate
1	412	50° 23.5485'N	110° 35.0061'W	Silt 100% 10 cm deep over gravel-cobble	Gravel +
2	1792	50° 23.5854'N	110° 35.1000'W	Gravel 95% Sand 5%	Gravel +
3	2205	50° 23.6094'N	110° 35.1066'W	Gravel 90% Sand 5% Silt 5%	Gravel +
4	4013	50° 23.6833'N	110° 35.0946'W	Boulder 40% Cobble 30% Gravel 20% Sand 10%	Gravel +
5	**5404**	**50° 23.7068'N**	**110° 35.2042'W**	**Sand 60% Gravel 40%**	**Gravel +**
7	5825	50° 23.7206'N	110° 35.2158'W	60% Sand 40% Gravel	Sand
8	6056	50° 23.7308'N	110° 35.2285'W	Gravel 70% Sand 30%	Gravel +
9	6832	50° 23.7989'N	110° 35.3667'W	Silt 98% Sand 2%	Silt
10	7385	50° 23.8172'N	110° 35.3721'W	Sand 100%	Sand
11	7732	50° 23.8407'N	110° 35.3961'W	Sand 100%	Sand
12	8643	50° 23.8802'N	110° 35.3498'W	Silt 100%	Silt
13	9281	50° 23.8948'N	110° 35.3665'W	Sand 50% Silt 50%	Silt
14	9786	50° 23.9013'N	110° 35.3687'W	Sand 40% Silt 40% Cobble 20%	Silt
15	**10567**	**50° 23.9784'N**	**110° 35.4538'W**	**Gravel 60% Sand 40%**	**Sand**
17	14228	50° 24.3780'N	110° 35.6046'W	Boulder 15% Cobble 60% Gravel 25% Gravel	Gravel +
18	14497	50° 24.3942'N	110° 35.6168'W	Boulder 15% Cobble 60% Gravel 25%	Gravel +
19	15684	50° 24.5657'N	110° 35.5869'W	Boulder 15% Cobble 55% Gravel 25% Sand 5%	Gravel +
20	15990	50° 24.5815'N	110° 35.5837'W	Boulder 15% Cobble 55% Gravel 25% Sand 5%	Gravel +

Table 3-3. Adult, juvenile and total positions within and outside of the study area during the study period.

	Study site (n)	Other (n)	Portion found at study site (%)
Adults	23	34	40.4%
Juveniles	3	26	10.3%
Total	26	60	30.23%

Table 3-4. Permuted ANOVA results, mean total daily movement (km).

Factor	Df	Sum Sq	Mean Sq	F value	Prob(param)	p
Diel	1	20372.05	20372.1	0.356	0.551	0.579
Diel (Res)	358	20477995	57201.1			
Ice on/off	1	12118786	1.2E+07	113.816	<0.001	<0.001
Ice on/off (Res)	178	18952927	106477			
Monthly	1	6.303	6.303	33.335	<0.001	<0.001
Monthly (Res)	178	33.655	0.189			
Juv/Adult	1	60316.09	60316.1	0.421	0.517	0.519
Juv/Adult (Res)	361	51745466	143339			

Table 3-5. Permuted ANOVA results, mean daily depth (m).

Factor	Df	Sum Sq	Mean Sq	F value	Prob(param)	p
Diel	1	0.343	0.343	1.539	0.215	0.227
Diel (Res)	358	79.786				
Ice on/off	1	1.761	1.761	9.806	0.002	0.003
Ice on/off (Res)	188	31.977				
Monthly	1	12.245	12.245	101.412	<0.001	<0.001
Monthly (Res)	178	21.493				
Juv/Adult	1	0.996	0.996	2.646	0.104	0.106
Juv/Adult (Res)	361	135.969				

Table 3-6. Permuted ANOVA results, aggregation (daily total grid cells occupied).

Factor	Df	Sum Sq	Mean Sq	F value	Prob(param)	P
Diel	1	0.005	0.005	0.001	0.966	0.962
Diel (Res)	358	1014.521				
Ice on/off	1	22.581	22.581	9.545	0.002	0.003
Ice on/off (Res)	188	444.717				
Monthly	1	130.843	130.843	70.442	< 0.001	< 0.001
Monthly (Res)	178	330.628				
Monthly Diel	1	202.611	202.611	67.262	< 0.001	< 0.001
Monthly Diel (Res)	361	1087.415				

Table 3-7. CART-derived predictive variables and preference direction for selected collective position periods as identified by recursive partitioning.

Percentile	Period	Branch	Variable 1	Variable 2	Variable 3	Threshold(s)
Core	Ice On	1	Depth	NA	NA	>2.6
Range	Ice On	1	Depth	NA	NA	>2.8
		2	Depth	Depth STD	NA	<2.8, >0.14
Core	Ice Off	1	Depth STD	NA	NA	>0.13
		2	Depth STD	Depth	NA	<0.13, >3.3
Range	Ice Off	1	Depth	NA	NA	>2.8
		2	Depth	Depth STD	NA	<2.8, >0.13
Core	Day	1	Depth	NA	NA	>2.8
		2	Depth	Depth STD	NA	<2.8, >0.13
Range	Day	1	Depth	NA	NA	>2.8
		2	Depth	Depth STD	NA	<2.8, >0.13
Core	Night	1	Depth	NA	NA	>2.8
		2	Depth	Depth STD	NA	<2.8, >0.13
Range	Night	1	Depth	NA	NA	>3
		2	Depth	Depth STD	NA	<3, <0.15
Core	All	1	Depth	NA	NA	>2.8
		2	Depth	Depth STD	NA	<2.8, <0.13
Range	All	1	Depth	NA	NA	>3
		2	Depth	Depth STD	NA	<3, <0.13

Table 3-8. CART-derived predictive variables and selection direction for monthly collective position periods as identified by recursive partitioning.

Percentile	Period	Branch	Variable 1	Variable 2	Variable 3	Threshold(s)
Core	November	1	Depth	NA	NA	>2.8
			Depth	Bottom Velocity	NA	<2.8, <0.76
Range	November	1	Depth	NA	NA	>2.8
Core	December	1	Depth	NA	NA	>2.8
			Depth	Bottom Velocity	NA	<2.8, <0.55
Range	December	1	Depth	NA	NA	>2.8
Core	January	1	Depth	NA	NA	>2.8
			Depth	Bottom Velocity	NA	<2.8, <0.55
Range	January	1	Depth	NA	NA	>2.9
Core	February	1	Depth	NA	NA	>2.9
			Depth	Bottom Velocity	NA	<2.9, <0.56
Range	February	1	Depth	NA	NA	>2.8
Core	March	1	Depth	NA	NA	>2.8
Range	March	1	Depth	NA	NA	>2.8
		2	Depth	Depth STD	NA	<2.8, >0.13
Core	April	1	Depth STD	NA	NA	>0.13
Range	April	1	Depth STD	NA	NA	>0.13
		2	Depth STD	Depth	NA	<0.13, >1.2
		3	Depth STD	Depth STD	Bottom Velocity	<0.13, <1.2, <0.55

Table 3-9. Spearman correlation of variables. Multicollinearity among predictor variables occurs due to a latent common factor. By and large, substrate, depth, and bottom velocity are all influenced by the force of moving water on the underlying geological structure over time. Sandy substrate and depth (in bold) approached the 0.80 threshold (Ruppert *et al.*, 2009) suggesting a sizeable correlation and high collinearity between these variables.

	Substrate (gravel)	Substrate (silt)	Bottom Velocity, STD	Depth, STD	Bottom Velocity, mean	Substrate (sand)	Depth, mean
Substrate (gravel)	1.00						
Substrate (silt)	-0.32	1.00					
Bottom Velocity, STD	0.06	-0.05	1.00				
Depth, STD	-0.13	-0.04	0.17	1.00			
Bottom Velocity, mean	-0.39	-0.17	0.21	0.21	1.00		
Substrate (sand)	-0.56	-0.46	0.03	0.27	0.56	1.00	
Depth, mean	-0.72	-0.10	-0.02	0.27	0.60	**0.79**	1.00

Table 3-10. Broad-scale depths in reaches of the South Saskatchewan River system. Few fluvial locations, (approximately 5.7%) of available habitat possess depths > 3.5 m. Lake Diefenbaker is located ~400 river kilometers from the study site. Depth data courtesy of Doug Watkinson, personal communication, June 30, 2016.

Bin	Oldman	South Saskatchewan	Lake Diefenbaker	Oldman %	South Saskatchewan %	Lake Diefenbaker %
-8.5	0	109	236	0.00%	0.03%	1.37%
-8	0	83	79	0.00%	0.02%	0.46%
-7.5	0	161	64	0.00%	0.04%	0.37%
-7	0	247	76	0.00%	0.07%	0.44%
-6.5	0	457	89	0.00%	0.13%	0.52%
-6	0	641	63	0.00%	0.18%	0.37%
-5.5	0	1051	38	0.00%	0.29%	0.22%
-5	0	1788	198	0.00%	0.49%	1.15%
-4.5	3	2790	465	0.00%	0.77%	2.70%
-4	15	4657	702	0.01%	1.28%	4.08%
-3.5	105	8804	1134	0.08%	2.42%	6.60%
-3	345	16498	1151	0.26%	4.53%	6.70%
-2.5	1229	30710	1805	0.93%	8.44%	10.50%
-2	2813	51029	2236	2.12%	14.02%	13.01%
-1.5	7576	74125	2849	5.71%	20.37%	16.57%
-1	17942	78503	2375	13.52%	21.58%	13.82%
-0.5	102694	92192	3631	77.38%	25.34%	21.12%

3.7 Figures

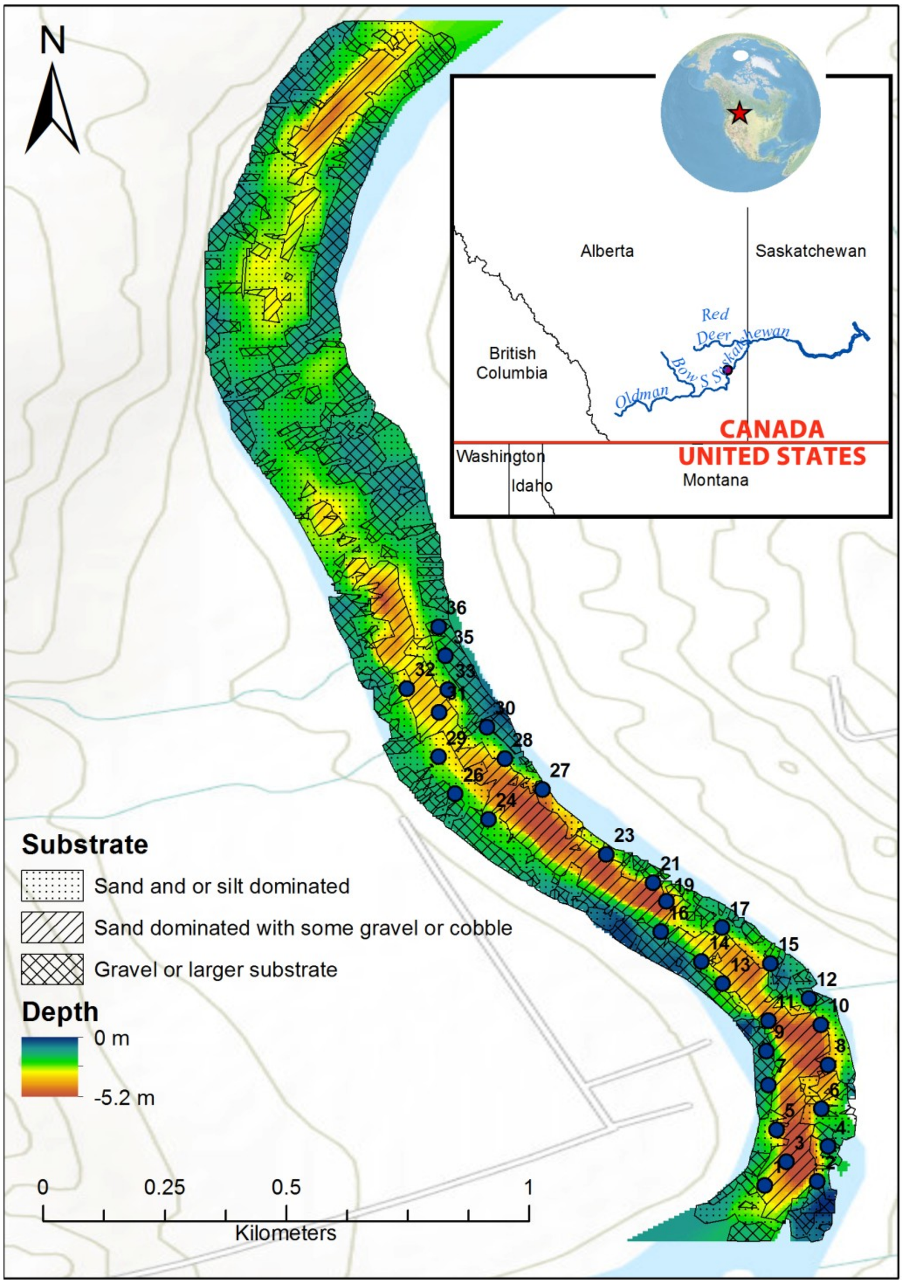


Figure 3-1. Study area showing recovered co-located receiver/sync tag pairs. Cross-hatch areas represent gravel and larger substrate, parallel lines represent sand-dominated substrate with some gravel or cobble, and dots represent silt-dominated substrate. Inset: provincial and global locator.

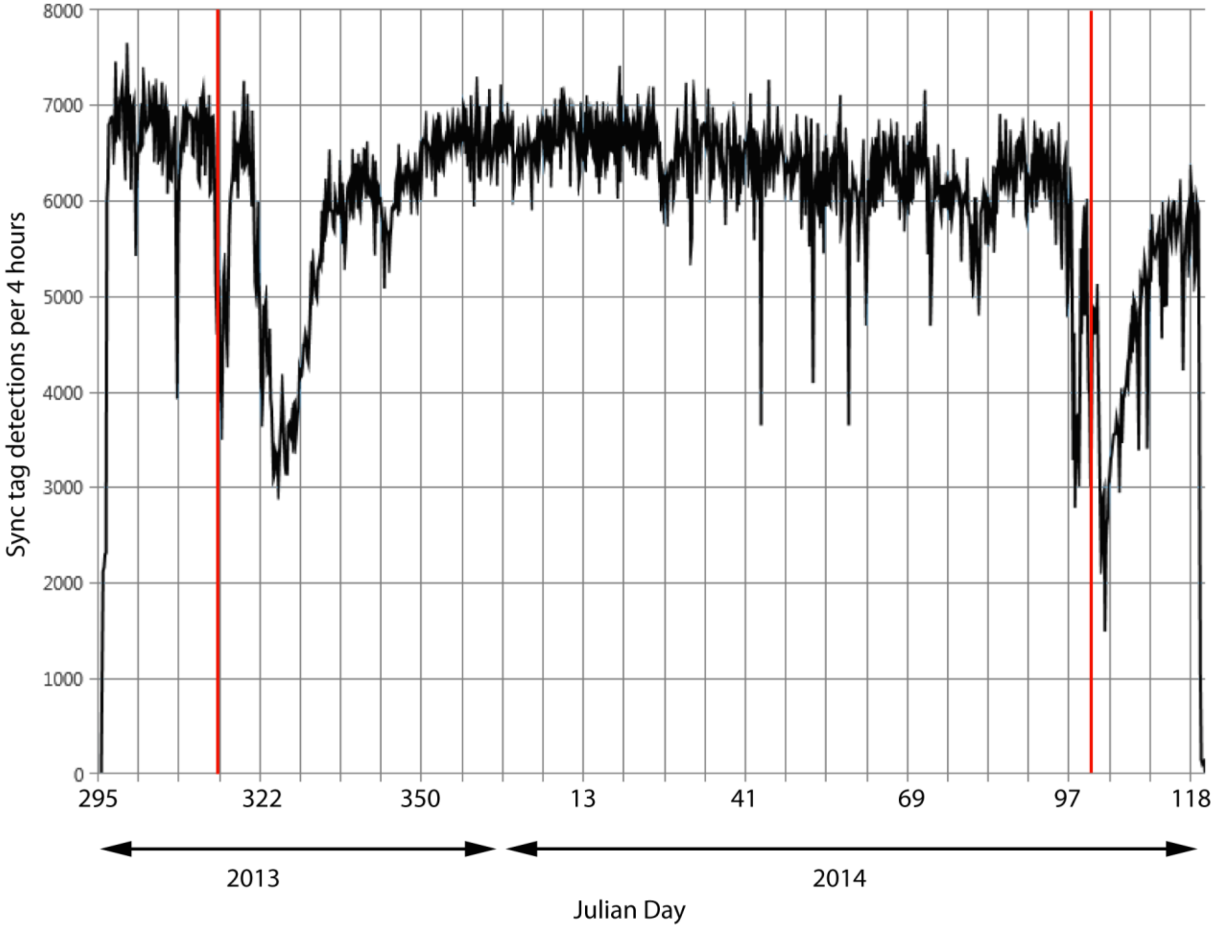


Figure 3-2. Total sync tag detections for the study period. Detection numbers are binned into 4 hour intervals. Left red bar indicates beginning of ice-on period at Julian day 314 (2013), right red bar indicates end of ice-on period at Julian day 99 (2014).

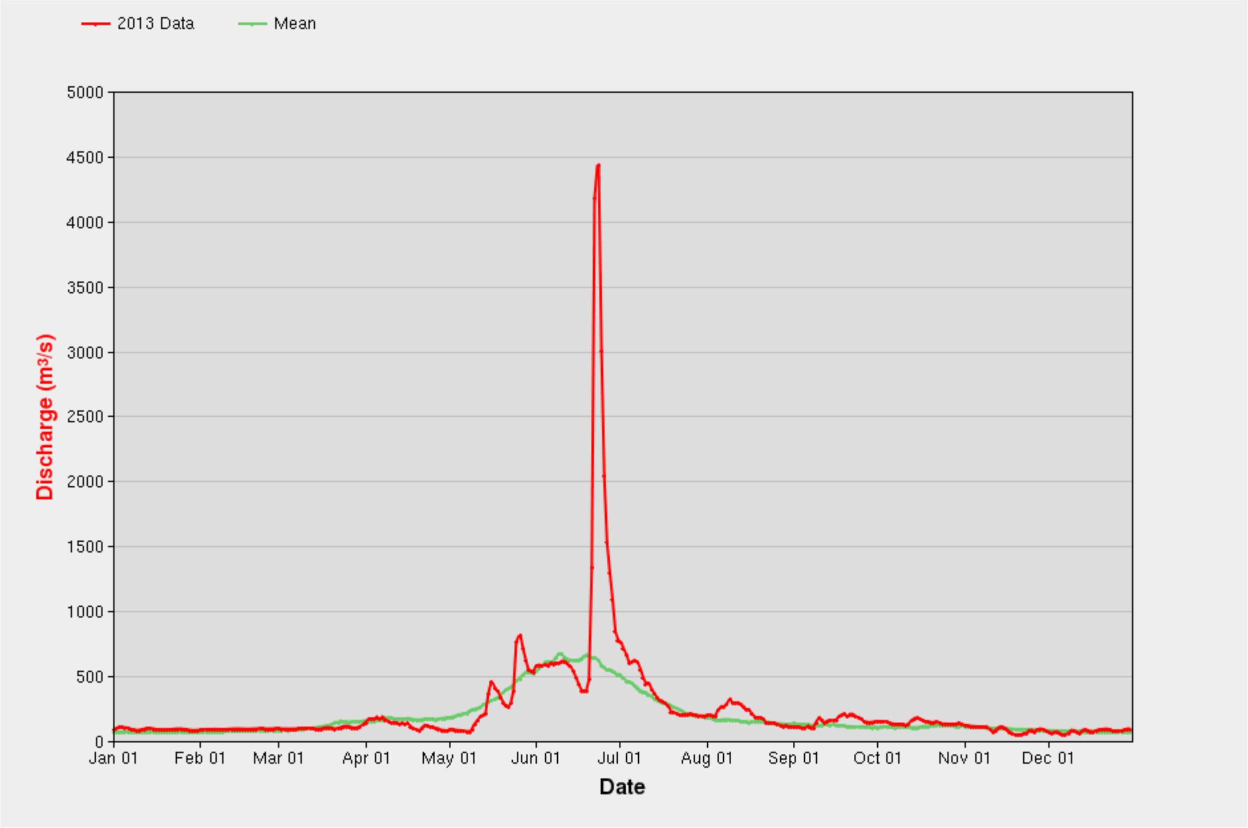


Figure 3-3. River flow rates (m^3/s) for the South Saskatchewan River at Medicine Hat Station (05AJ001, lat/lon 50° 02' 31" N/110° 40' 39" W). The red curve indicates 2013 flow rates; green curve indicates the 106 year average flow rates.

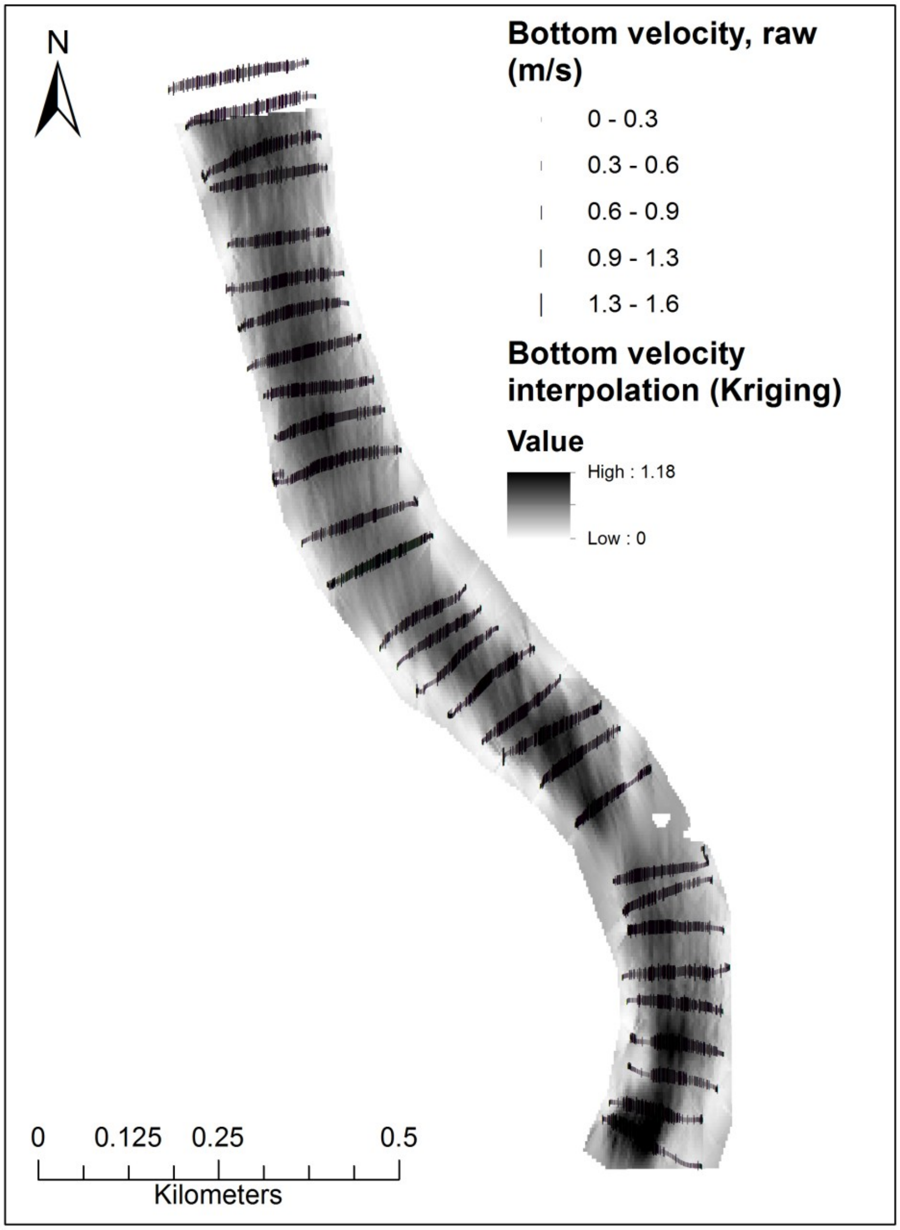


Figure 3-4. Krig interpolation and River Surveyor transects highlighting bottom velocity (m/s). Erroneously high values at transect terminals were addressed by use of moving average corrections prior to interpolation.

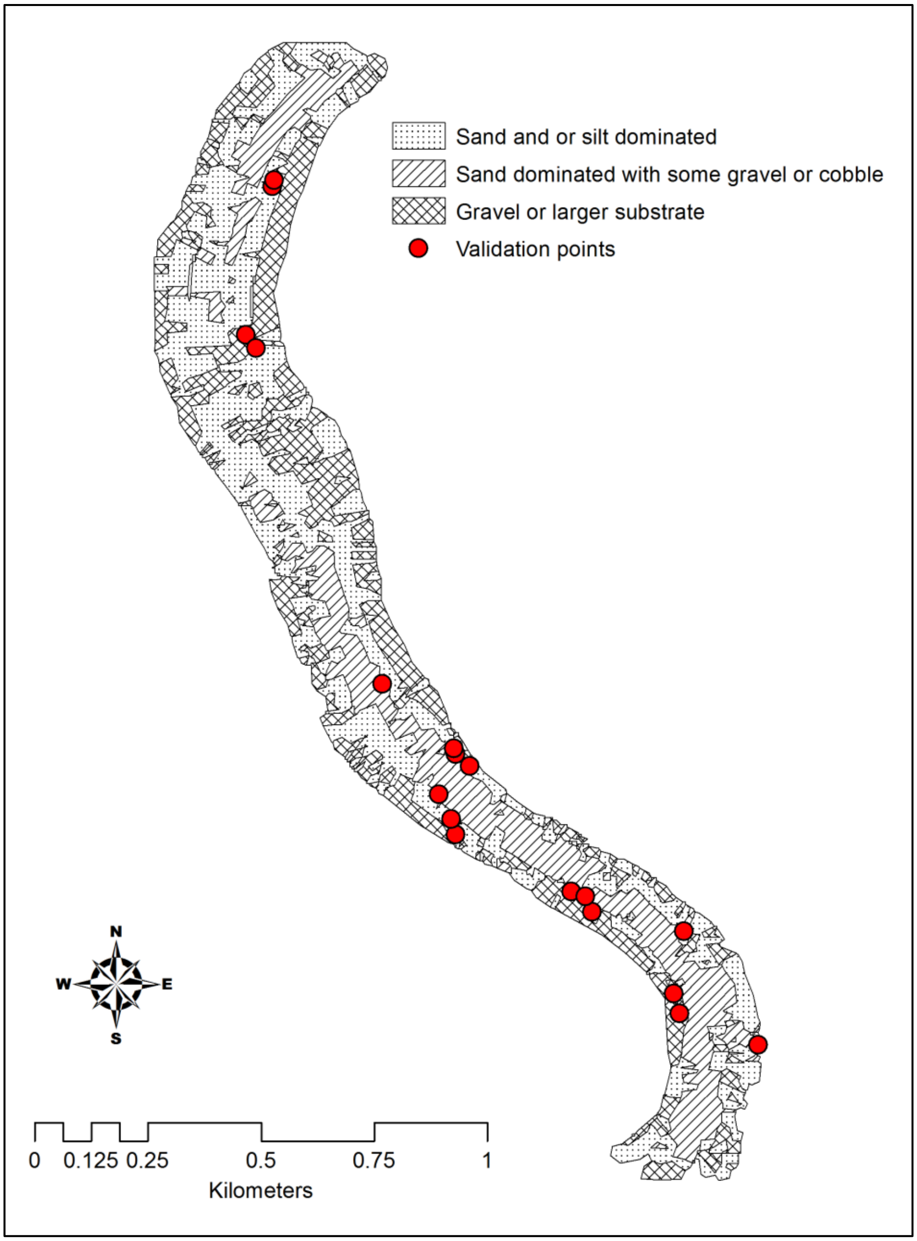


Figure 3-5. Substrate validation point locations compared to interpolated substrate values.

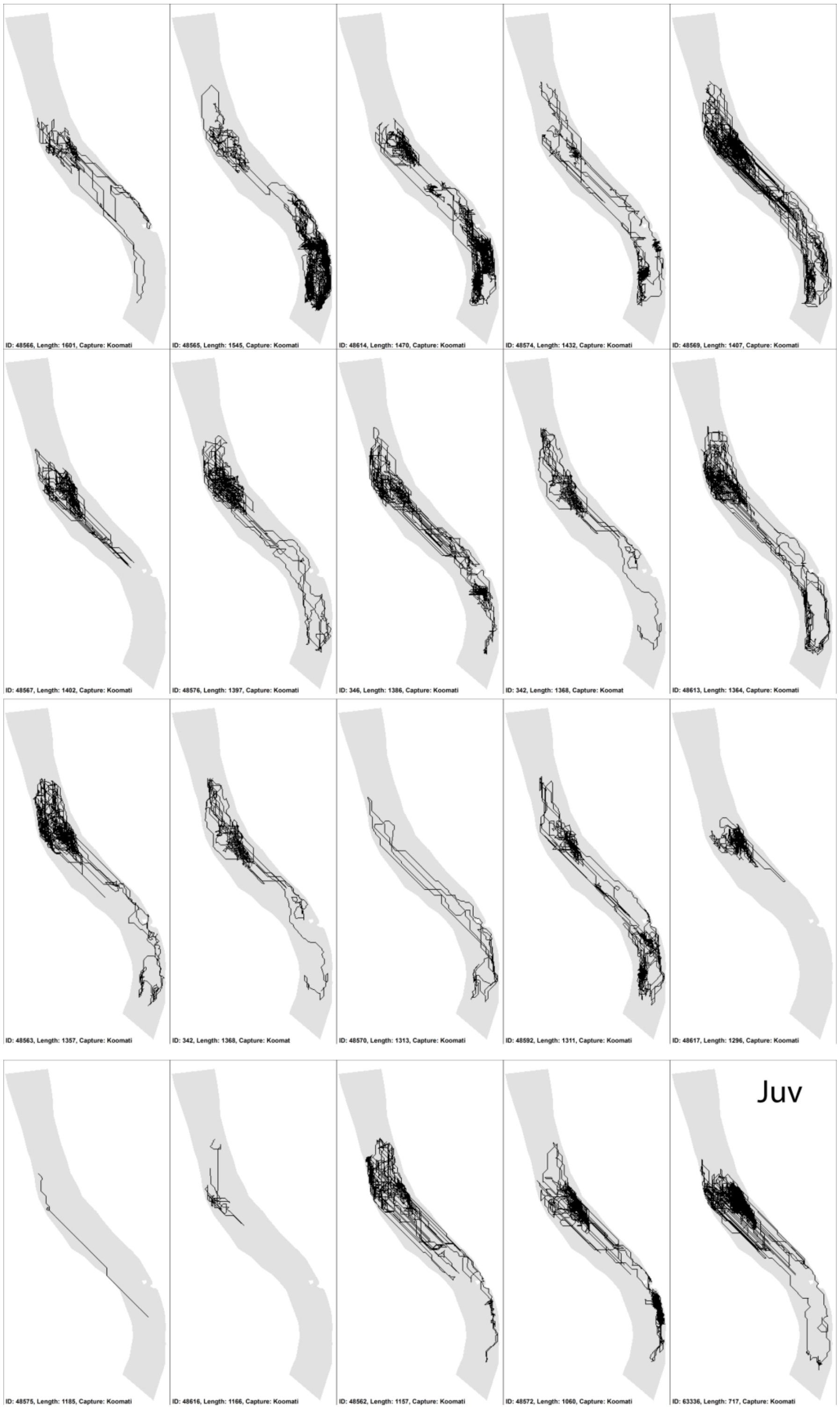


Figure 3-6. Paths of study site-captured fish, ordered (top to bottom, left to right) by total length (mm).

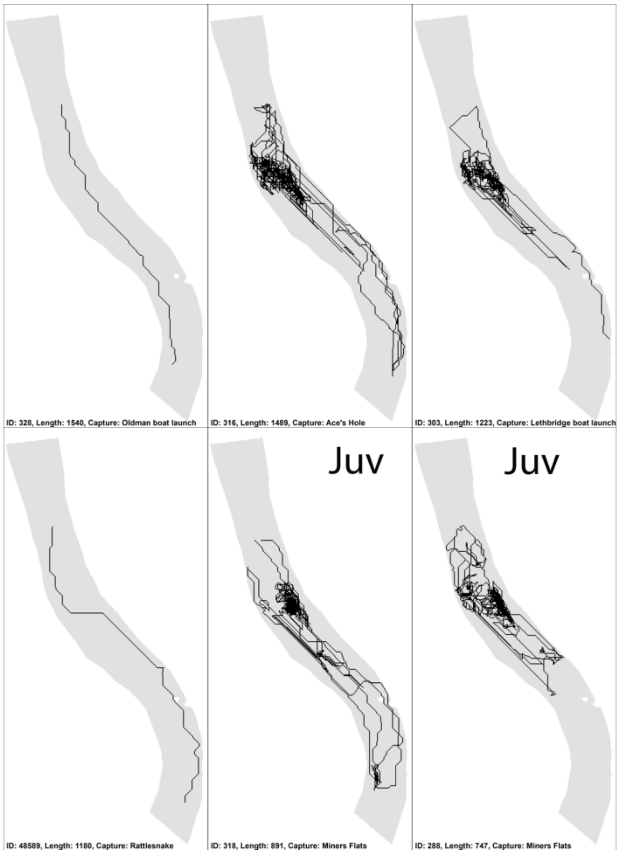


Figure 3-7. Paths of fish captured outside of study site, ordered (top to bottom, left to right) by total length (mm). Individuals were considered juveniles if adjusted total length measured < 1150 mm (Lacho, 2013).

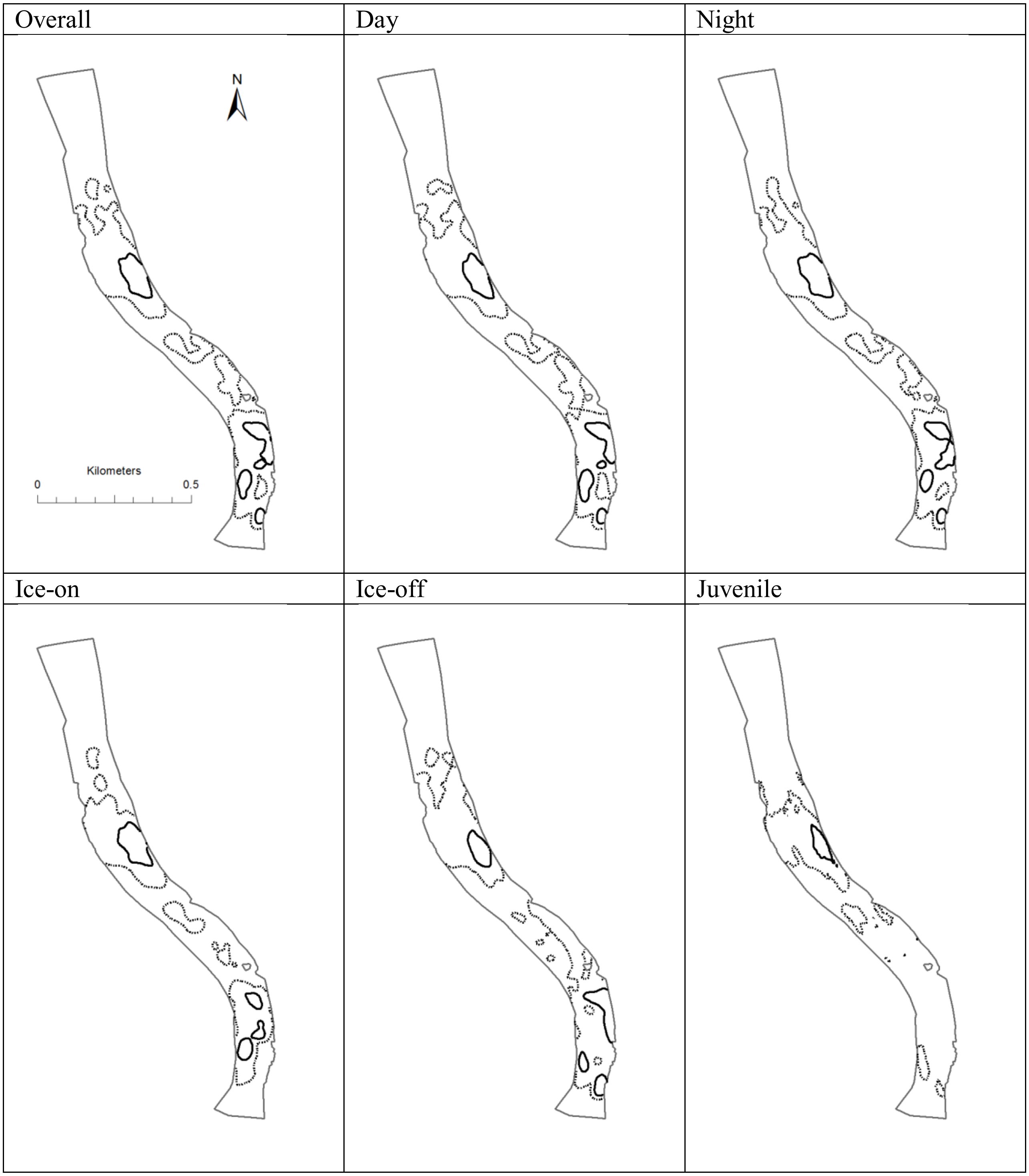


Figure 3-8. Panel map showing core and range kernel densities for overall, diel, ice-on/off, and juveniles. Black outline indicates core range (50th percentile), broken line indicates range (95th percentile). Study area is outlined in gray.

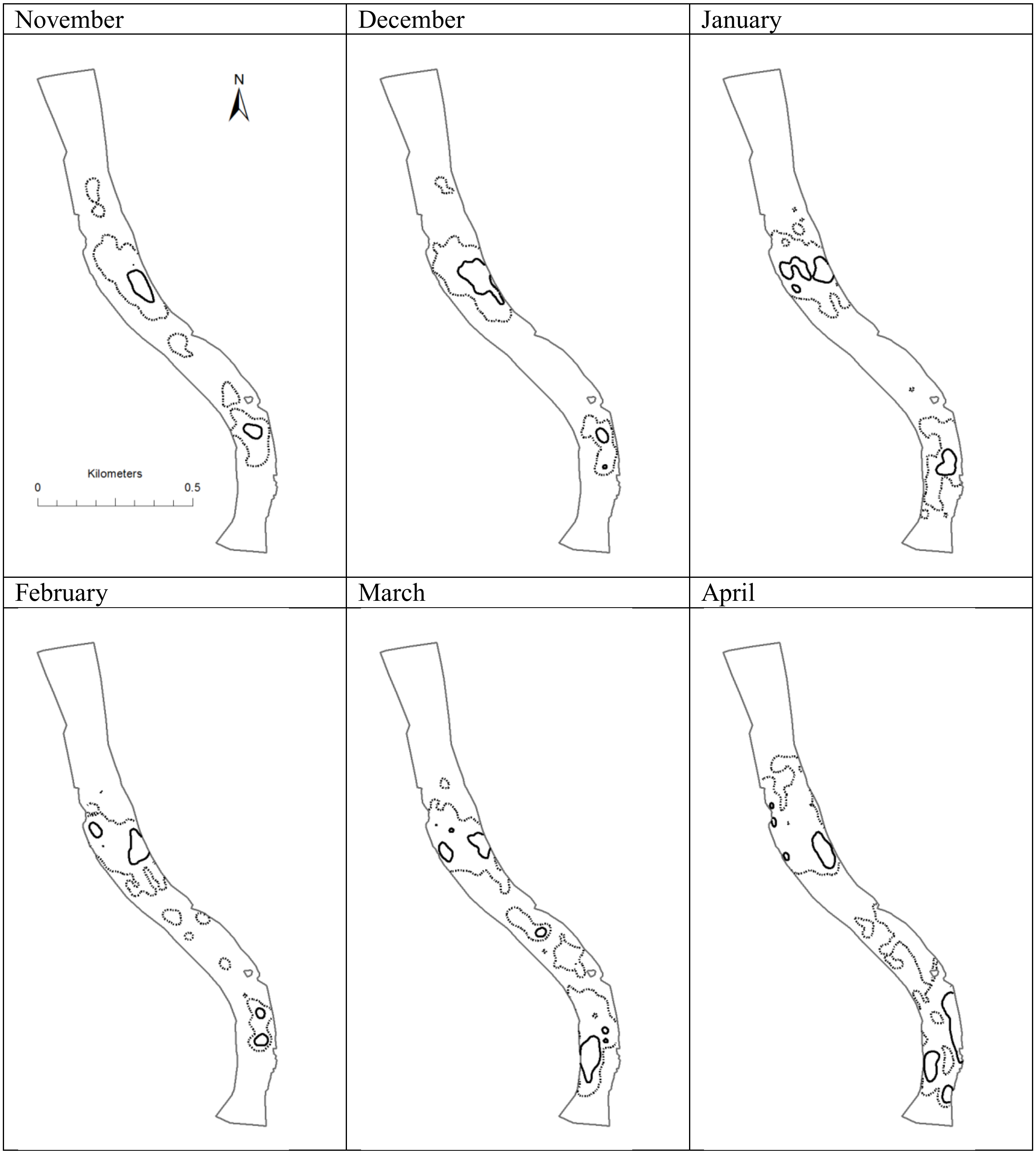


Figure 3-9. Panel map showing monthly core and range kernel density maps. Black outline indicates core range (50th percentile), broken line indicates range (95th percentile). Study area is outlined in gray.

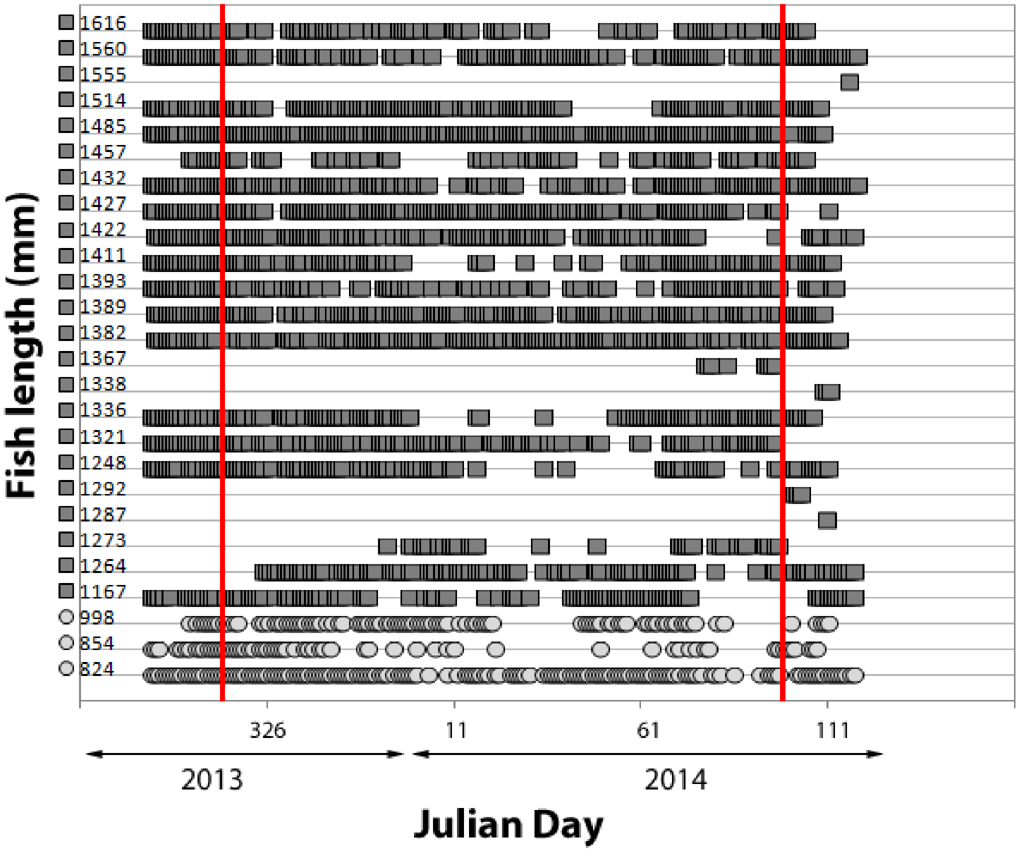


Figure 3-10. Daily detections for 26 fish with >1 detection during the study period, ordered by total length. Juveniles are indicated by circular markers. Left red bar indicates beginning of ice-on period at Julian day 314 (2013), right red bar indicates end of ice-on period at Julian day 99 (2014). Individuals not present during all months of the study period were excluded from analysis.

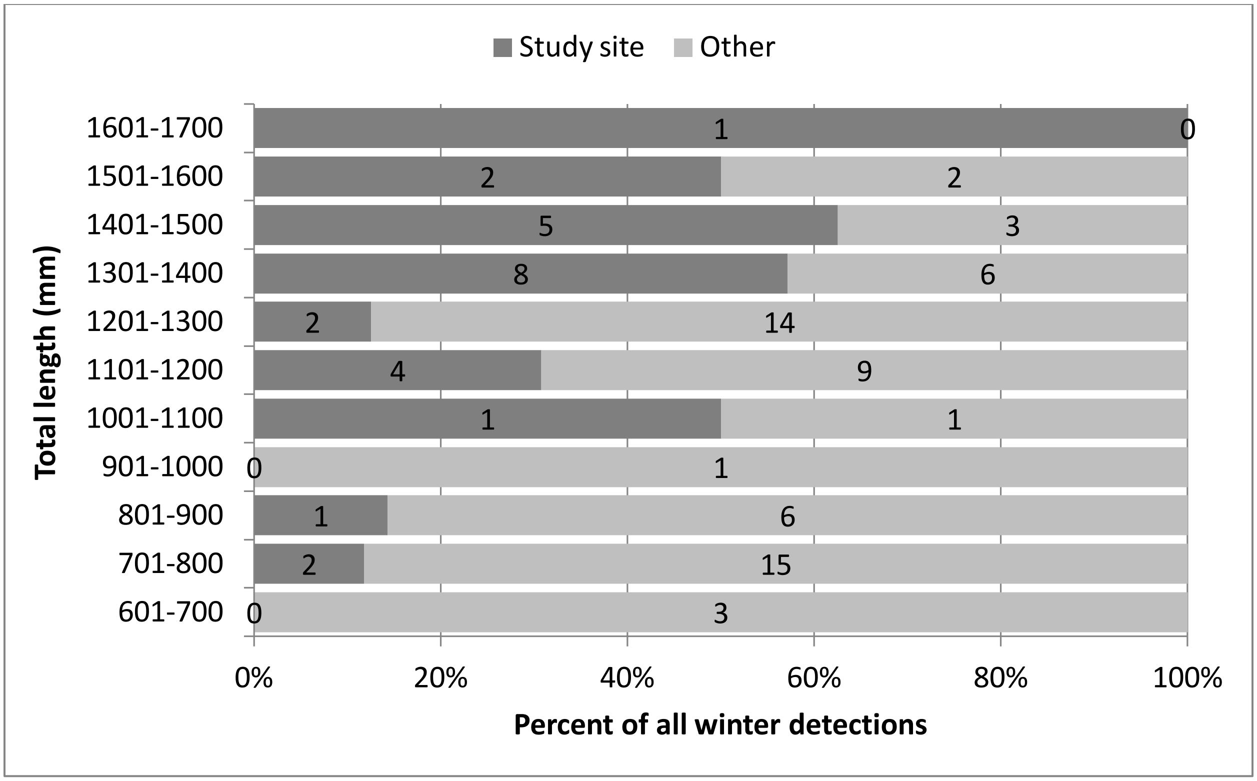


Figure 3-11. Proportional comparison of total length (mm) for Lake Sturgeon overwintering at South Saskatchewan River winter study site (n=26) compared to all other monitored locations within the South Saskatchewan River Basin (n=60) for the period October 22, 2013 to April 30, 2014.

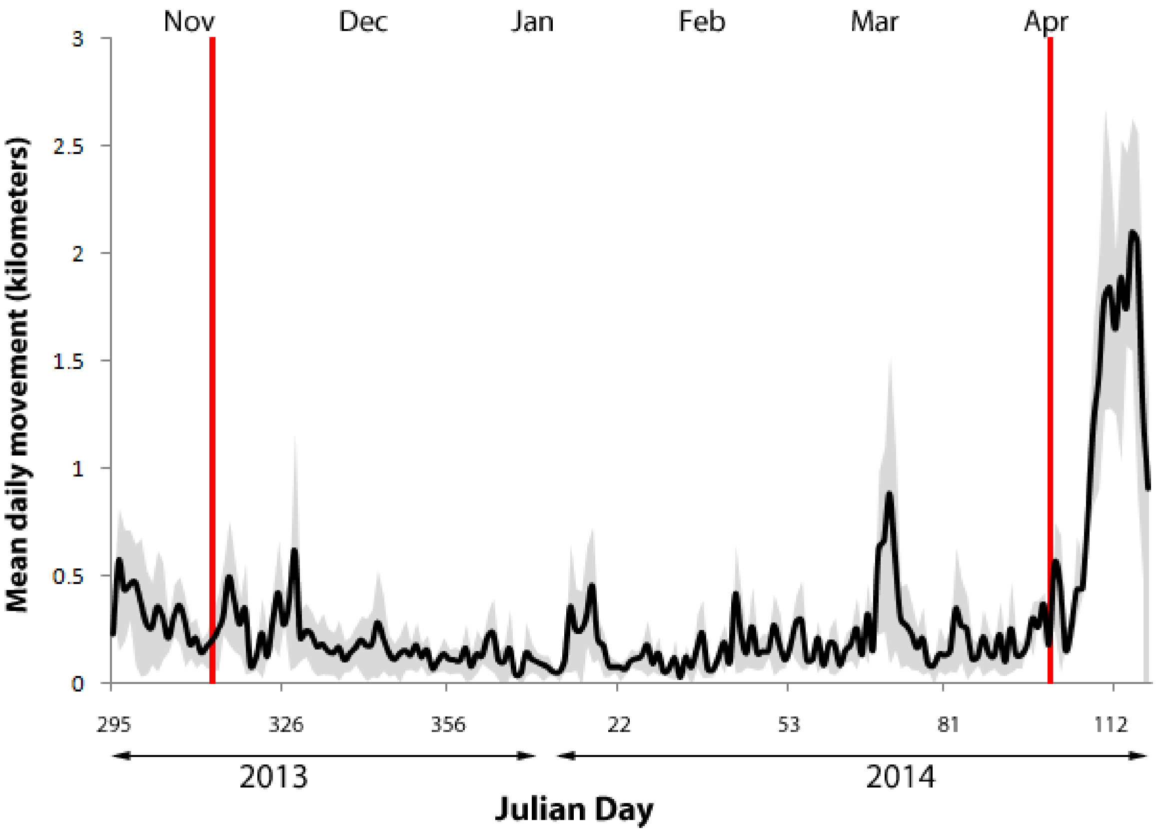


Figure 3-12. Mean daily movement per fish in kilometers by Julian day. Solid line indicates average daily movement per fish (kilometers); gray area indicates one standard deviation about the mean. Left red bar indicates beginning of ice-on period at Julian day 314 (2013), right red bar indicates end of ice-on period at Julian day 99 (2014).

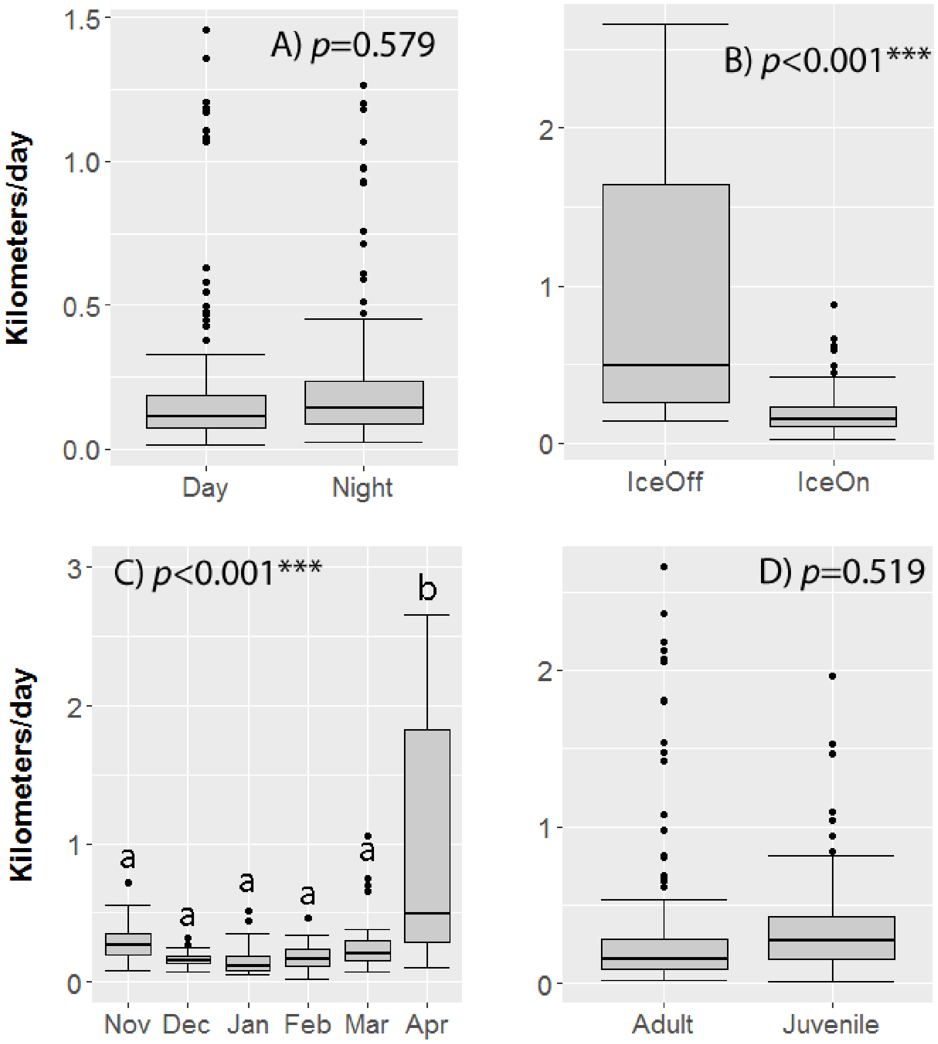


Figure 3-13. Daily total movement (km) per individual averaged for (left to right, top to bottom) A) diel, B) ice-on and ice-off and C) monthly periods; and D) comparing movement of juveniles to adults during the entire study period. Individuals were considered juveniles if adjusted total length measured < 1150 mm (Lacho, 2013). Letters over monthly boxes indicate significant relationships among factors as identified by post-hoc Tukey analysis. Means that do not share a letter are significantly different.

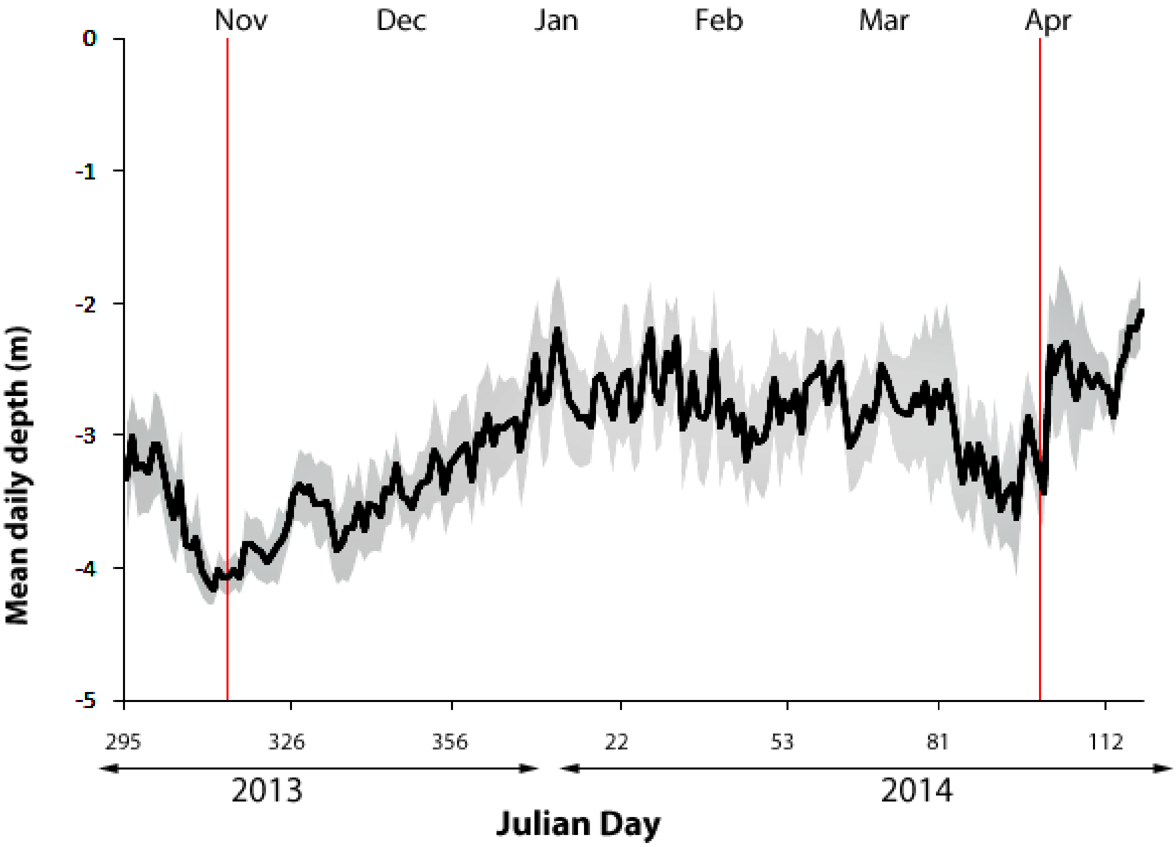


Figure 3-14. Mean daily depth (m) of river at sturgeon positions. Solid line indicates average daily river depths selected (meters); gray area indicates one standard deviation about the mean. Left red bar indicates beginning of ice-on period at Julian day 314 (2013), right red bar indicates end of ice-on period at Julian day 99 (2014).

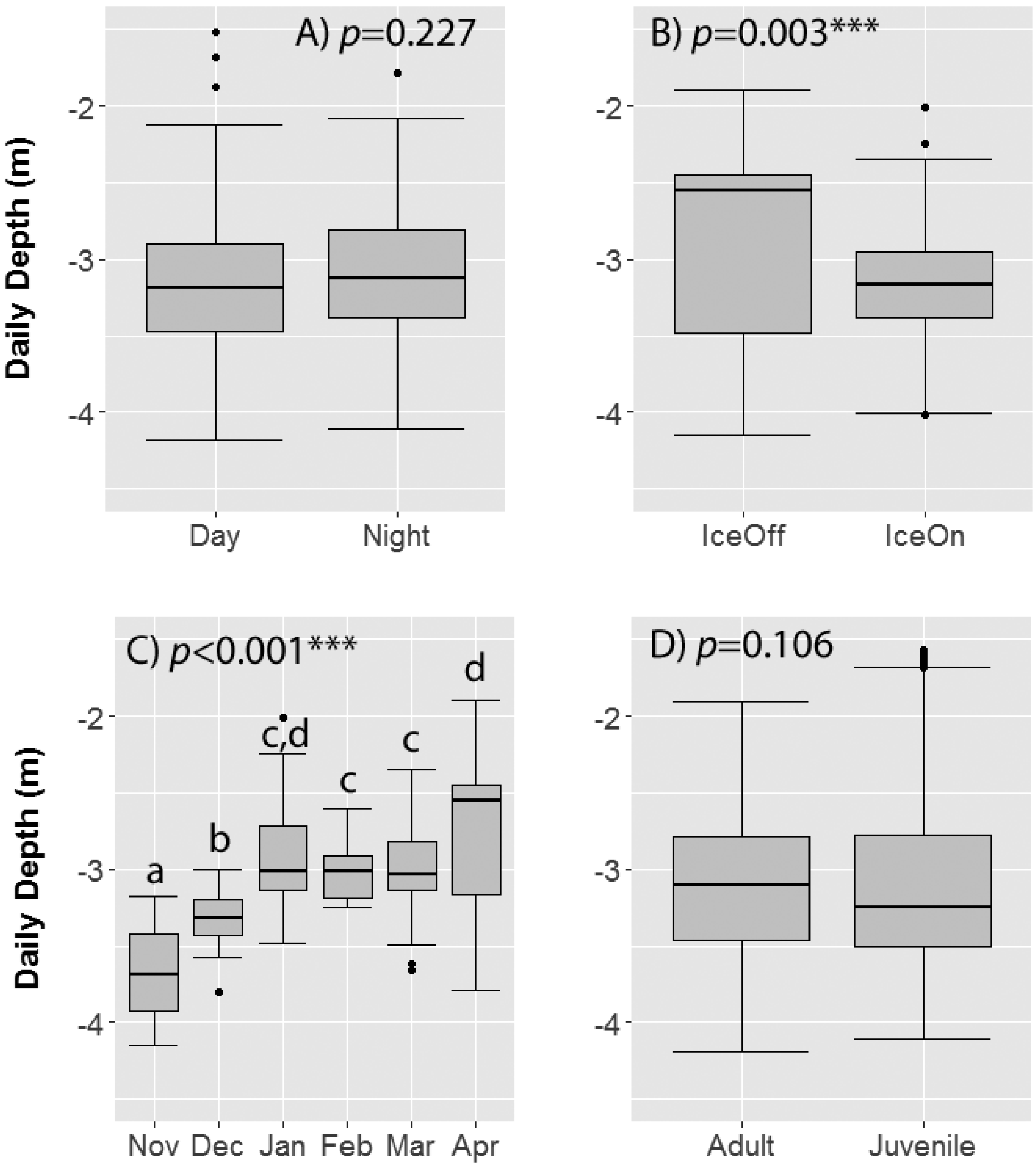


Figure 3-15. Daily depth (m) averaged for (left to right, top to bottom) A) diel, B) ice-on and ice-off, and C) monthly periods; and D) comparing movement of juveniles to adults during the entire study period. Individuals were considered juveniles if adjusted total length measured < 1150 mm (Lacho, 2013). Depth measurements collected were corrected by Letters over monthly boxes indicate significant relationships among factors as identified by post-hoc Tukey analysis. Means that do not share a letter are significantly different.

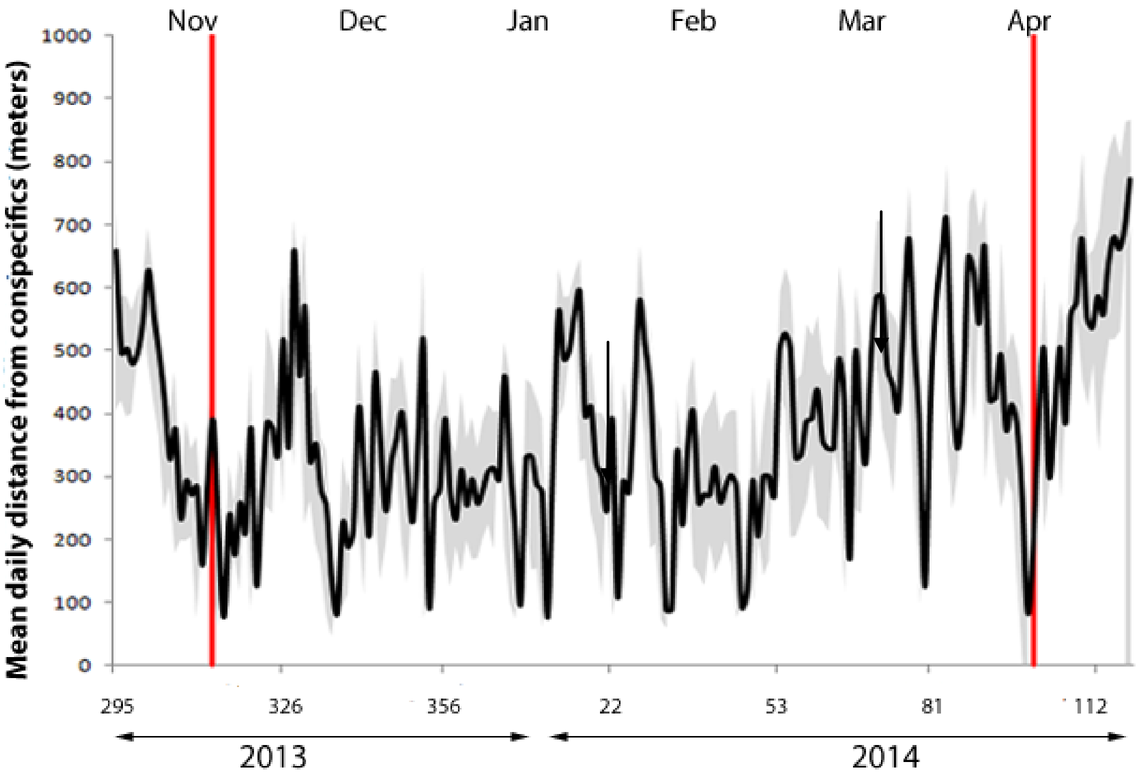


Figure 3-16. Mean distances among individuals (m) used to determine aggregation as measured by mean daily distance from target fish to conspecific positions using paired (target fish, all other fishes) XY coordinates. Differences in distance among individuals are not apparent except during ice formation and breakup periods, when distances decrease. Left red bar indicates beginning of ice-on period at Julian day 314 (2013), right red bar indicates end of ice-on period at Julian day 99 (2014).

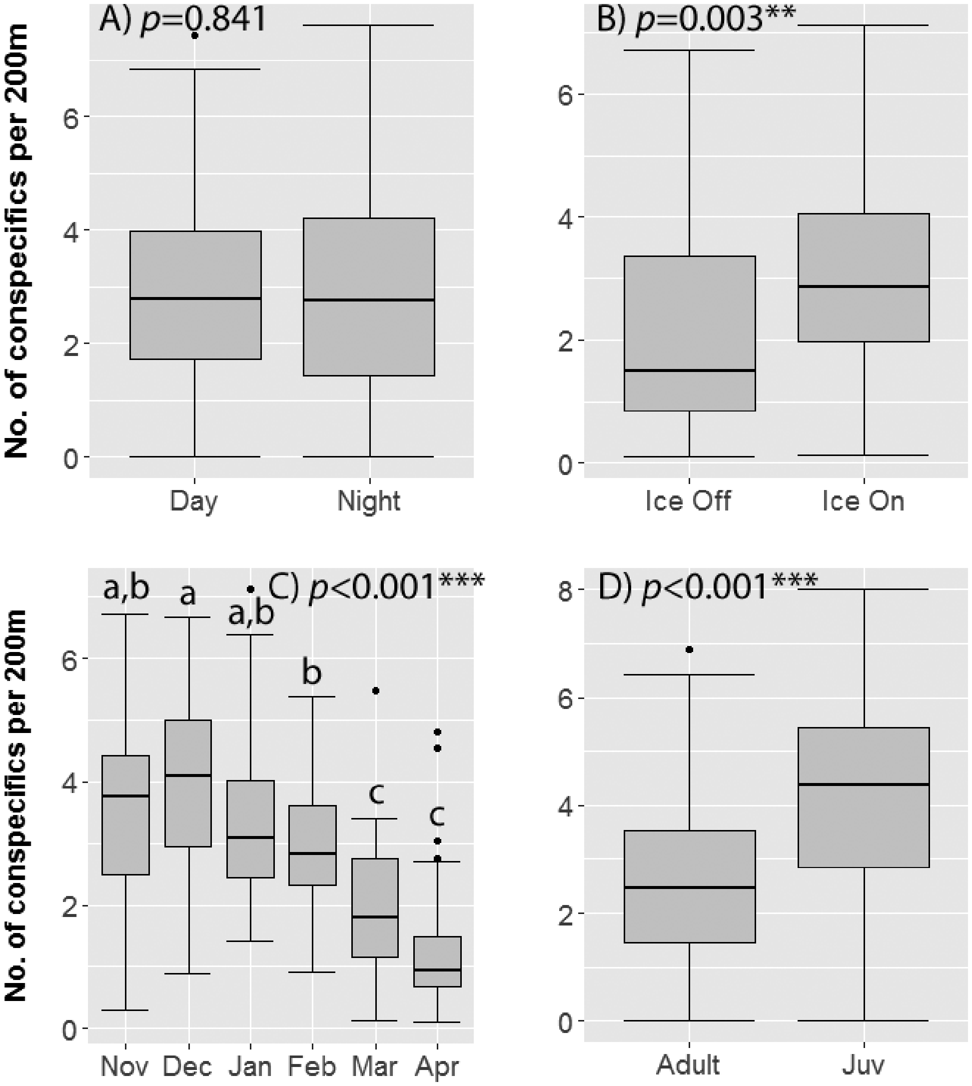


Figure 3-17. Aggregation as determined by the number of conspecifics detected within the 10th percentile (200m) distance from the target individual for (left to right, top to bottom) A) diel, B) ice-on and ice-off, and C) monthly periods; and D) comparing movement of juveniles to adults during the entire study period. Individuals were considered juveniles if adjusted total length measured < 1150 mm (Lacho, 2013). Letters over monthly and monthly diel boxes indicate significant relationships among factors as identified by post-hoc Tukey analysis. Means that do not share a letter are significantly different.

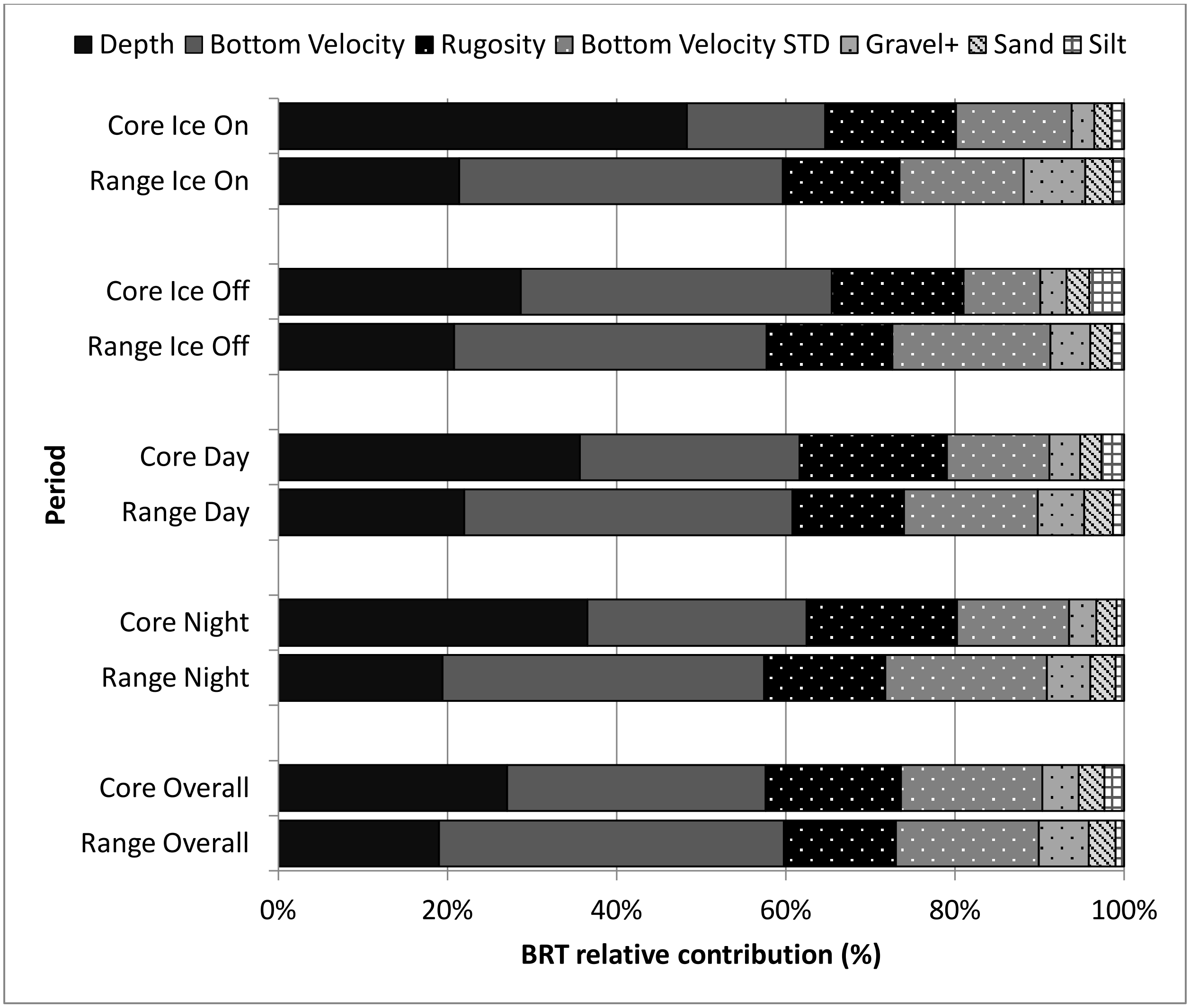


Figure 3-18. Boosted Regression Tree (BRT) presence/absence predictor contributions for core and range spatial limits within ice on/off, diel, and overall periods. Solid black bar indicates depth (m), black bar with white stipples indicates rugosity (depth standard deviation); gray bar indicates bottom velocity (m/s), gray bar with white stipples indicates bottom turbulence (bottom velocity standard deviation). White bar with black stipples indicates silt-dominated substrate, parallel lines indicates sandy substrate, cross-hatch lines gravel and larger substrate.

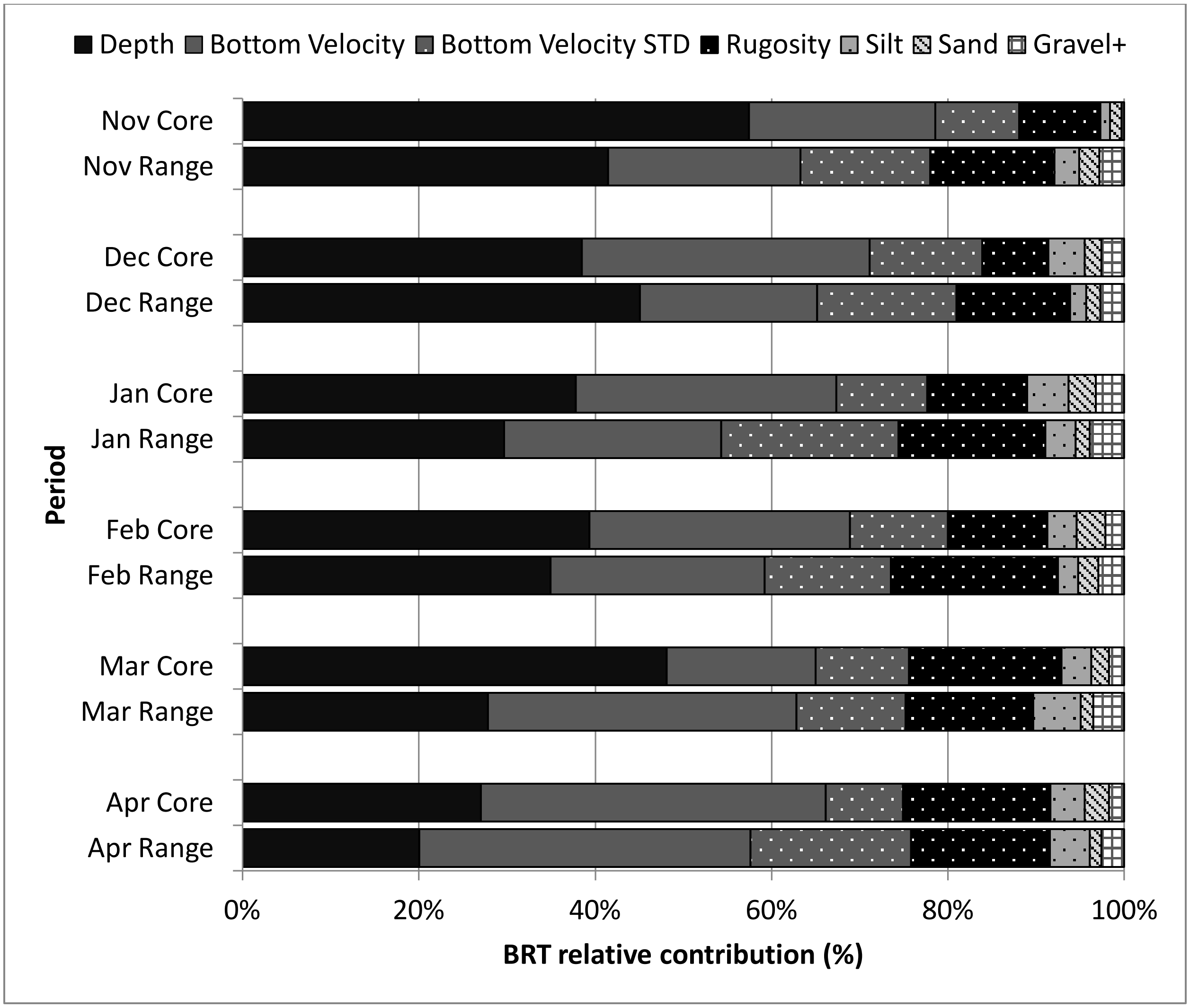


Figure 3-19. Boosted Regression Tree (BRT) relative contributions for core and range spatial limits for monthly periods. Solid black bar indicates depth (m), black bar with white stipples indicates rugosity (depth standard deviation); gray bar indicates bottom velocity (m/s), gray bar with white stipples indicates bottom velocity standard deviation. White bar with black stipples indicates silt-dominated substrate, parallel lines sandy substrate, cross-hatch lines gravel and larger substrate.

3.8 Appendices

Appendix 3-1. Historical daily discharge at South Saskatchewan River at Medicine Hat Station (05AJ001, lat/lon 50° 02' 31" N/110° 40' 39" W).

October	Flow (m^3/s)	April	Flow (m^3/s)
10/01/2013	151	04/01/2014	139
10/02/2013	154	04/02/2014	149
10/03/2013	151	04/03/2014	157
10/04/2013	152	04/04/2014	158
10/05/2013	150	04/05/2014	158
10/06/2013	143	04/06/2014	159
10/07/2013	136	04/07/2014	161
10/08/2013	133	04/08/2014	169
10/09/2013	131	04/09/2014	221
10/10/2013	132	04/10/2014	293
10/11/2013	129	04/11/2014	339
10/12/2013	125	04/12/2014	429
10/13/2013	132	04/13/2014	446
10/14/2013	162	04/14/2014	406
10/15/2013	176	04/15/2014	366
10/16/2013	179	04/16/2014	333
10/17/2013	170	04/17/2014	292
10/18/2013	160	04/18/2014	269
10/19/2013	152	04/19/2014	259
10/20/2013	150	04/20/2014	248
10/21/2013	146	04/21/2014	251
10/22/2013	145	04/22/2014	249
10/23/2013	151	04/23/2014	248
10/24/2013	143	04/24/2014	252
10/25/2013	134	04/25/2014	249
10/26/2013	134	04/26/2014	254
10/27/2013	133	04/27/2014	255
10/28/2013	133	04/28/2014	255
10/29/2013	132	04/29/2014	265

Appendix 3-2. Model fit parameters of boosted regression tree (BRT) analyses.

Percentile	Period	Sample Size (cells)	Trees	Mean Deviance	Residual Mean Deviance	CV ROC score	SE (CV ROC score)
Core	Nov	638	1850	1.115	0.655	0.865	0.01
	Dec	574	1850	1.061	0.68	0.829	0.011
	Jan	694	1800	1.166	0.753	0.794	0.007
	Feb	561	1000	1.045	0.729	0.789	0.012
	Mar	937	1400	1.311	0.894	0.791	0.008
	Apr	1201	1600	1.384	1.11	0.726	0.01
	Ice On	1234	1200	1.385	0.941	0.797	0.008
	Ice Off	1238	1100	1.386	1.052	0.735	0.009
	Day	1353	1700	1.381	1.036	0.757	0.013
	Night	1352	1400	1.382	1.038	0.772	0.009
	All	1497	1250	1.35	0.97	0.764	0.005
Range	Nov	1355	1750	1.383	0.896	0.802	0.007
	Dec	1149	1350	1.375	0.969	0.778	0.005
	Jan	1182	1450	1.382	0.971	0.738	0.005
	Feb	995	1400	1.337	0.881	0.775	0.008
	Mar	1503	1250	1.348	0.942	0.782	0.011
	Apr	1673	1300	1.261	0.8	0.79	0.009
	Ice On	1648	1600	1.259	0.884	0.772	0.006
	Ice Off	1714	1200	1.236	0.771	0.804	0.011
	Day	1724	1150	1.23	0.771	0.809	0.009
	Night	1739	1200	1.225	0.773	0.802	0.007
	All	1761	1000	1.203	0.766	0.803	0.01

Appendix 3-3. BRT primary predictive variables and percent deviance explained by predictors.

Percentile	Period	Primary Predictor	Relative contribution (%)
Core	Nov	Depth	57.4
	Dec	Depth	38.6
	Jan	Depth	37.8
	Feb	Depth	39.4
	Mar	Depth	48.2
	Apr	Bottom Velocity	39.2
	Ice On	Depth	48.4
	Ice Off	Bottom Velocity	36.8
	Day	Depth	35.6
	Night	Depth	36.6
	Overall	Bottom Velocity	30.6
Range	Nov	Depth	41.5
	Dec	Depth	45.1
	Jan	Depth	29.7
	Feb	Depth	34.9
	Mar	Bottom Velocity	35
	Apr	Bottom Velocity	37.6
	Ice On	Bottom Velocity	38.3
	Ice Off	Bottom Velocity	37
	Day	Bottom Velocity	38.8
	Night	Bottom Velocity	38
	Overall	Bottom Velocity	40.8

Appendix 3-4. BRT level 2 predictive variables and percent deviance explained by predictors.

Percentile	Period	Level 2 Predictor	Relative contribution (%)
Core	Nov	Bottom Velocity	21.1
	Dec	Bottom Velocity	32.7
	Jan	Bottom Velocity	29.5
	Feb	Bottom Velocity	29.6
	Mar	Rugosity	17.3
	Apr	Depth	27.1
	Ice On	Bottom Velocity	16.4
	Ice Off	Depth	28.7
	Day	Bottom Velocity	25.9
	Night	Bottom Velocity	25.9
	Overall	Depth	27.1
Range	Nov	Bottom Velocity	21.8
	Dec	Bottom Velocity	20.1
	Jan	Bottom Velocity	24.6
	Feb	Bottom Velocity	24.2
	Mar	Depth	27.9
	Apr	Depth	20.1
	Ice On	Depth	21.4
	Ice Off	Depth	20.8
	Day	Depth	22
	Night	Depth	19.4
	Overall	Depth	19

Appendix 3-5. BRT level 3 predictive variables and percent deviance explained by predictors.

Percentile	Period	Level 3 Predictor	Relative contribution (%)
Core	Nov	Bottom Velocity STD	9.5
	Dec	Bottom Velocity STD	12.8
	Jan	Rugosity	11.3
	Feb	Rugosity	11.3
	Mar	Bottom Velocity	16.9
	Apr	Rugosity	16.7
	Ice On	Rugosity	15.5
	Ice Off	Rugosity	15.6
	Day	Rugosity	17.4
	Night	Rugosity	17.8
	Overall	Bottom Velocity STD	16.7
Range	Nov	Bottom Velocity STD	14.7
	Dec	Bottom Velocity STD	15.8
	Jan	Bottom Velocity STD	20.1
	Feb	Rugosity	18.9
	Mar	Rugosity	14.5
	Apr	Bottom Velocity STD	18.2
	Ice On	Bottom Velocity STD	14.7
	Ice Off	Bottom Velocity STD	18.7
	Day	Bottom Velocity STD	15.8
	Night	Bottom Velocity STD	19.1
	Overall	Bottom Velocity STD	16.9

Appendix 3-6. BRT level 4 predictive variables and percent deviance explained by predictors.

Percentile	Period	Level 4 Predictor	Relative contribution (%)
Core	Nov	Rugosity	9.2
	Dec	Rugosity	7.5
	Jan	Bottom Velocity STD	10.3
	Feb	Bottom Velocity STD	11.1
	Mar	Bottom Velocity STD	10.6
	Apr	Bottom Velocity STD	8.8
	Ice On	Bottom Velocity STD	13.7
	Ice Off	Bottom Velocity STD	9.1
	Day	Bottom Velocity STD	12.1
	Night	Bottom Velocity STD	13.3
	Overall	Rugosity	16
Range	Nov	Rugosity	14.1
	Dec	Rugosity	12.9
	Jan	Rugosity	16.7
	Feb	Bottom Velocity STD	14.3
	Mar	Bottom Velocity STD	12.4
	Apr	Rugosity	15.8
	Ice On	Rugosity	13.8
	Ice Off	Rugosity	14.9
	Day	Rugosity	13.2
	Night	Rugosity	14.3
	Overall	Rugosity	13.2

Appendix 3-7. BRT level 5 predictive variables and percent deviance explained by predictors.

Percentile	Period	Level 5 Predictor	Relative contribution (%)
Core	Nov	Rugosity	9.2
	Dec	Rugosity	7.5
	Jan	Bottom Velocity STD	10.3
	Feb	Bottom Velocity STD	11.1
	Mar	Bottom Velocity STD	10.6
	Apr	Bottom Velocity STD	8.8
	Ice On	Bottom Velocity STD	13.7
	Ice Off	Bottom Velocity STD	9.1
	Day	Bottom Velocity STD	12.1
	Night	Bottom Velocity STD	13.3
	Overall	Rugosity	16
Range	Nov	Rugosity	14.1
	Dec	Rugosity	12.9
	Jan	Rugosity	16.7
	Feb	Bottom Velocity STD	14.3
	Mar	Bottom Velocity STD	12.4
	Apr	Rugosity	15.8
	Ice On	Rugosity	13.8
	Ice Off	Rugosity	14.9
	Day	Rugosity	13.2
	Night	Rugosity	14.3
	Overall	Rugosity	13.2

Appendix 3-8. BRT level 6 predictive variables and percent deviance explained by predictors.

Percentile	Period	Level 6 Predictor	Relative contribution (%)
Core	Nov	Sand	1.3
	Dec	Silt	4.1
	Jan	Silt	4.7
	Feb	Silt	3.3
	Mar	Silt	3.4
	Apr	Silt	3.9
	Ice On	Silt	2.7
	Ice Off	Sand	4.1
	Day	Silt	3.6
	Night	Silt	3.2
	Overall	Silt	4.3
Range	Nov	Silt	2.8
	Dec	Gravel+	2.7
	Jan	Gravel+	3.9
	Feb	Gravel+	2.9
	Mar	Silt	5.4
	Apr	Silt	4.5
	Ice On	Silt	7.3
	Ice Off	Silt	4.7
	Day	Silt	5.5
	Night	Silt	5.1
	Overall	Silt	5.9

Appendix 3-9. BRT least predictive variables and percent deviance explained by predictors.

Percentile	Period	Level 7 Predictor	Relative contribution (%)
Core	Nov	Gravel or larger	0.6
	Dec	Gravel or larger	1.9
	Jan	Sand	2.6
	Feb	Sand	1.9
	Mar	Sand	2
	Apr	Sand	1.3
	Ice On	Sand	1.2
	Ice Off	Sand	2.1
	Day	Sand	1.5
	Night	Sand	1.1
	Overall	Sand	0.7
Range	Nov	Sand	2.3
	Dec	Sand	1.1
	Jan	Sand	0.6
	Feb	Sand	1.6
	Mar	Sand	1.6
	Apr	Sand	1.1
	Ice On	Sand	1.6
	Ice Off	Sand	1.6
	Day	Sand	1.2
	Night	Sand	1.4
	Overall	Sand	1.5

Chapter Four: **Thesis Summary**

Sturgeon are considered to be more critically endangered than any other group of species on earth (Carpenter, 2010). As a family, they pre-date birds and flowering plants; as a genus, they have survived meteor events, ice ages, and mass extinctions. They are highly fecund, long-lived, with a robust digestive system allowing for diverse feeding preferences, and, in the long-term, have been able to adapt to a variety of dissimilar environments (Auer, 1996). The attributes associated with large body size that contribute to sturgeon's high fecundity, namely slow maturation, intermittent spawning periodicity, and broad migration capacity have provided sturgeon the ability to survive for millions of years, but now contribute to their decline (Carlander, 1947; Birstein, 1993). Anthropogenic habitat change, waterway fragmentation, and direct predation (including angling) by human beings for their commercially valuable roe have driven most sturgeon populations to near extinction (Musick *et al*., 2000; Pikitch *et al*., 2005).

Alberta Lake Sturgeon (*Acipenser fulvescens*) have been more fortunate; they have been the subject of conservation efforts for many years (McLeod *et al*., 1999), and by some accounts, their populations are rebounding (Alberta Lake Sturgeon Recovery Team, 2011). Ensuring continued survival of this distinctive species requires protection of their critical habitat and mitigation of threats throughout their life cycle. Altered hydrology (floods, drought) due to human activity and climate change pose threats to their habitat. Knowledge gaps described in the Alberta Lake Sturgeon Recovery Plan identify a series of priority research goals. The intention of this study is to address these goals by a) assessing the impact of a severe flood on Lake Sturgeon health and behavior, and how this ecological disturbance affects a critical spawning habitat, and; b) developing a quantitative understanding of habitat use and movement behavior over winter, a lengthy and particularly challenging phase of the species' life cycle.

In Chapter 1 of this thesis, I described the species in terms of its morphology, life and natural history, and taxonomy and classification. I described the importance of the species to scientific research as an outgroup for molecular phylogenetics studies and as an environmental indicator species. Population declines, threats, conservation status, and recovery efforts were identified, with special emphasis on the study population in DU2/MU2, in Alberta. Study goals aligned with recovery plan knowledge gaps. Chapter 2 provided analysis and documentation of the impact of disturbance in the form of a large flood on Lake Sturgeon spawning habitat, and fine-scale movement responses of sturgeon during periods of extreme peak flow, addressing knowledge gap 4.4, Threats (Alberta Lake Sturgeon Recovery Team, 2011), specifying the need for information on stressors. Chapter 3 provided analysis and documentation of overwintering movement rates, depth selection, aggregation behavior and habitat selection by adult and juvenile Lake Sturgeon, which addresses knowledge gap 4.1, Biology (Alberta Lake Sturgeon Recovery Team, 2011), specifying the need for studies regarding winter distribution. Both study goals address knowledge gap 4.2, Habitat (Alberta Lake Sturgeon Recovery Team, 2011), specifying the need for an understanding of seasonal distribution and habitat use, critical to achieving judicious habitat protection.

In Chapter 2, I discussed the impact of a large-scale flood on critical Lake Sturgeon spawning habitat and behavior. In the South Saskatchewan River Basin (SSRB), 74.58% of water allocations are licensed for irrigation, and total allocations under the Master Agreement on Apportionment agreement established among Alberta, Saskatchewan, Manitoba and the federal government in 1969 exceeded Alberta's available share of the flow in dry years (Pentney and Ohrn, 2008). This problem was addressed in 1999, and resulted in the 1999 proclamation of the Alberta Water Act, which included a greater emphasis on protecting aquatic ecosystems (Pentney and Ohrn, 2008), and proportional allocation, rather than prior appropriation allocation, determination of usage rights during water shortage years (Rood and Vandersteen, 2010). Abundant scientific evidence suggests that with warming and increased evapotranspiration, disturbance events such as flooding and drought will become more common (Fisher *et al*., 2010). Indeed, the 2013 flood is the second "100-year flood" to strike Alberta in 20 years, the previous 'flood of the century' occurring in 1995 (Rood *et al*., 1998; Polzin and Rood, 2006). The 1995 "flood of the century" was followed by the 2000–2004 drought across western North America that produced pronounced terrestrial drying, river discharge reductions, and decreased cropland productivity (Schwalm *et al*., 2012). In 2015, drought conditions in Alberta became so severe that on August 21, 2015, the Alberta government declared the province an Agricultural Disaster Area (Minister of Agriculture and Agri-Food, 2016).

Though the 2013 flood did considerable damage in terms of human lives and infrastructure, claiming the lives of four people, displacing over 100,000 people (Environment Canada, 2014), and, as of February 2014, costing the government of Alberta $553 million in operating and $40 million in capital spending (Government of Alberta, 2014), it also improved substrate suitable for spawning, substantially increased heterogeneity as measured by patch density, and was well-tolerated by Lake Sturgeon residing in the South Saskatchewan River. Artificially-induced high velocity flows have been associated with physical injury, entrainment, and stranding in Lake Sturgeon, but in a natural habitat, Lake Sturgeon appear to be capable of evading damage by moving out of the main river channel to areas closer to the river's edge. Flood-induced changes in the benthic environment included de-siltation and increased heterogeneity, which have been shown to contribute to riverine biodiversity and macrobiotic community abundance (Meffe, 1984; Townsend *et al*., 1997; Snyder and Johnson, 2006). Siltation and homogeneity pose threats to critical habitat (Figure 4-1) that arise in regulated rivers and reduce resource abundance and diminish successful spawning (Auer, 1996; Bruch and Binkowski, 2002; Roseman *et al*., 2011). This study's findings support suggestions to re-establish seasonal high-flow regimes in regulated rivers (Stanford *et al*., 1996). This study is the first to investigate Lake Sturgeon responses to extreme flood conditions at a fine scale and *in situ*.

In Chapter 3, Lake Sturgeon overwintering movement, depth selection, aggregation behaviors and habitat selection choices were assessed, comprising the first fine-scale acoustic telemetry overwintering study of an entirely fluvial cohort of Lake Sturgeon. Of all sturgeon detected during the 6-month study period, 30% of them, which included 40% of all tagged adults (Table 3-3) were present at some point during the winter in this 1.5 kilometer stretch of river (equivalent to 0.14% of the habitat accessible to them), with 20 individuals detected throughout the study period. During this lengthy overwintering phase, Lake Sturgeon engaged in limited movement and increased aggregation, suggesting a limited resource (areas with sufficient depth) that could put Lake Sturgeon at risk if winter habitat is compromised. Study individuals showed a strong selection tendency toward deep habitat and low bottom velocities across all periods and percentiles.

4.1 Future research

Predicted increases in extreme, weather-related disturbance events include both floods and droughts, and dought may pose an even greater concern. Although Chapter 2 of this study focused on a peak flood event, droughts are likely to become more common. Lake Sturgeon showed superior adaptive responses to extreme high flow, but their large body size and migration requirements are not as well suited for conditions of extreme low water level and flow (Prosser, 1986). Future recommended work would include studying Lake Sturgeon behavior under low discharge and water level conditions linked to warming-induced increases in evapotranspiration and predicted increases in agricultural water use. Further work to identify key life-cycle stages and threats (Figure 4-1) should remain a high priority toward the conservation and recovery of Lake Sturgeon populations.

4.2 Figures

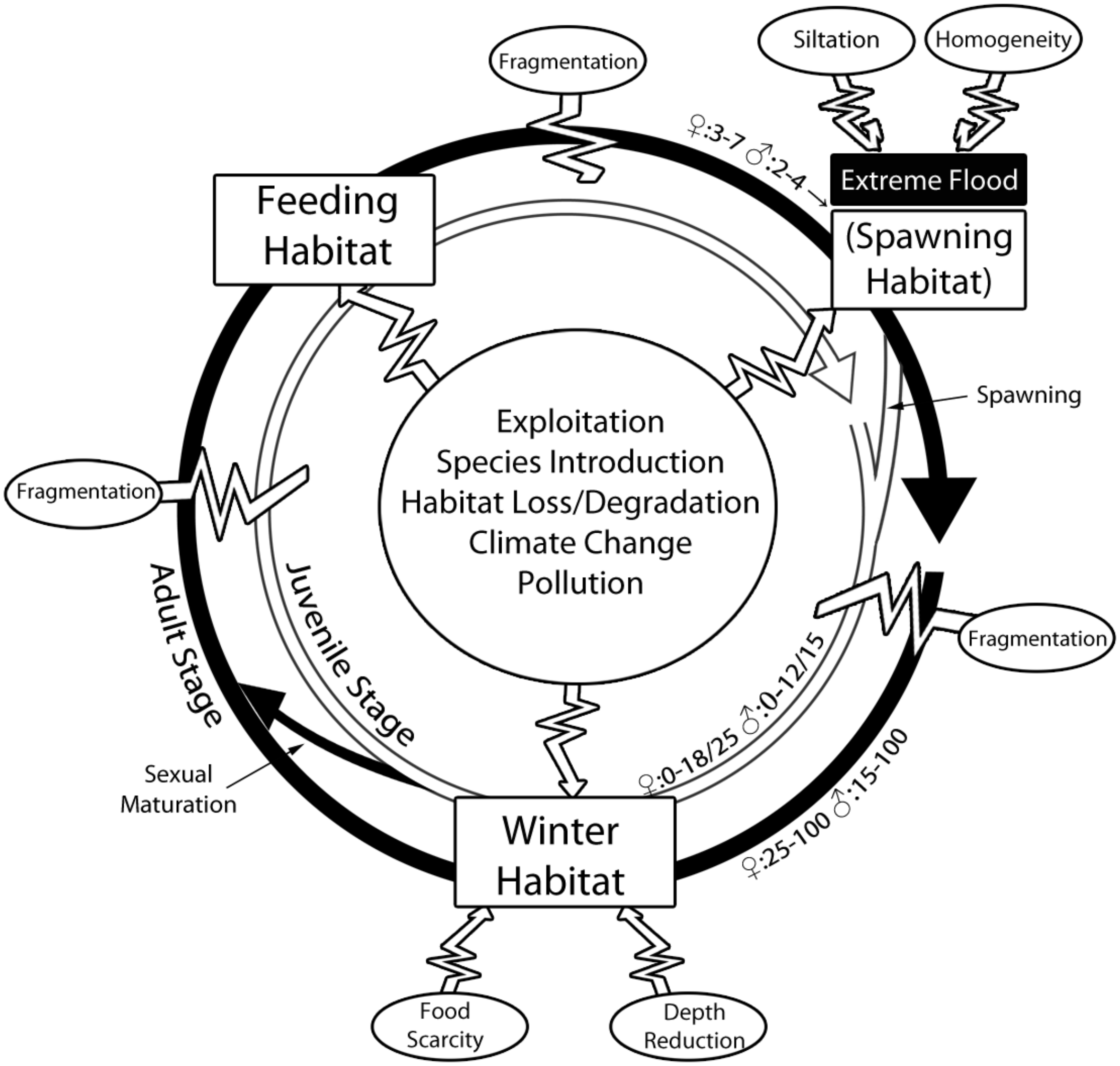


Figure 4-1. Post-analysis revised life-cycle diagram (Figure 1-3), with study findings included. Chapter 2 identified a beneficial impact of an extreme flood event on Lake Sturgeon spawning habitat, reducing siltation and increasing heterogeneity. Averted threats are indicated by bent arrows. Chapter 3 identified a lengthy seasonal phase of limited movement and increased aggregation, suggesting risk to Lake Sturgeon if winter habitat is compromised.

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