

Diagnosing causes of white sturgeon (*Acipenser transmontanus*)
recruitment failure and the importance of substrate condition to
yolksac larvae survival

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

Doctor of Philosophy

in

The Faculty of Graduate Studies
(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)
September 2012

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Abstract

White sturgeon are a conservation concern throughout their range, and three populations in Canada are experiencing nearly zero recruitment. While the presence of large dams on the Nechako, upper Columbia and Kootenay rivers suggests a causal relationship between flow regulation and recruitment failure, persistent uncertainty regarding the species' biology and its interaction with anthropogenic habitat change limits the understanding of the causal mechanisms of recruitment failure.

Recruitment failure causation in the Nechako and upper Columbia rivers was evaluated by comparing hindcasted recruitment with historical environmental changes. For the Nechako River population, recruitment failure coincided with substrate changes at a known spawning site; these changes were identified based on air photos and changes in river bed elevation. Evaluation of the upper Columbia River population considered the effects of multiple dams and other anthropogenic impacts, as well as the effects of sturgeon aging error and population structure. Eleven recruitment failure hypotheses were evaluated based on fifteen criteria, including stock specific temporal and spatial patterns of recruitment decline. Estimated timing of stock-specific recruitment declines was also compared with reach and watershed scale environmental changes and site-specific habitat changes. For both analyses, substrate change at spawning sites was identified as the likely cause of recruitment failure. Embryos and yolk sac larvae are expected to be the primary life stages affected in both cases.

Laboratory and field enclosure studies assessed the effects of substrate on drift, hiding and survival of yolk sac larvae. Contrary to many prior investigations, interstitial hiding was the predominant behaviour in laboratory studies in the presence of suitable interstitial habitat, and both

drift and predation by sculpins (*Cottus* spp.) increased when interstitial habitat was unavailable. Rapid and sustained hiding by yolk sac larvae and increased survival all suggest that hiding predominantly occurs in the vicinity of spawning habitat. Collectively my results indicate that recruitment failure results from increased early life history mortality in response to substrate changes at spawning sites. Increased survival of yolk sac larvae in response to gravel augmentation in field studies suggests that larger-scale substrate restoration at spawning sites provides a habitat based approach for recruitment restoration.

Preface

Portions of this thesis have been previously published in two articles. Chapter 2 is based on work that I undertook regarding analysis of historical changes in recruitment of white sturgeon in the Nechako River and the potential relationship to environmental changes. A version of Chapter 2 has been published as McAdam, S.O., C.J. Walters and C. Nistor. 2005. Linkages between white sturgeon (*Acipenser transmontanus*) recruitment and altered bed substrates in the Nechako River, Canada. *Trans. Am. Fish. Soc.* 134: 1448–1456. I conducted all of the biological analysis in this chapter and the entire write up. The air photo interpretation was led by me, but I received input from Craig Nistor. The specific gauge analysis was conducted by Craig Nistor.

A version of Chapter 4 has been published as McAdam, S.O. 2011. Behavioural responses of white sturgeon (*Acipenser transmontanus*) yolk sac larvae to substrate provide a potential mechanism of white sturgeon recruitment failure. *Can. J. Fish. Aquat. Sci.* 68: 812-822. I was responsible for the design, implementation and write up of all aspects of the laboratory work. Technical assistance was provided by Marcus Boucher.

This work was reviewed and approved by the Animal Care Committee application # A07-0162.

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Acknowledgements

Carl Walters has been an inspiration for many years and has influenced the way I think as a biologist. I'd like to thank him for his continued input, and for suggesting that I undertake this research as part of a Ph.D. program. My research committee has also provided important guidance and I sincerely thank its members for their input and interest. In particular I would like to thank Ted Down, who was key in providing the support of the B.C. Ministry of Environment, which allowed me to conduct this research. Eric Taylor, Mike Bradford and Villy Christensen all provided useful guidance throughout, and important guidance with respect to this thesis.

It is also very important to acknowledge the many people who are involved in recovery programs for white sturgeon, and have all helped in large and small ways. In particular I'd like to thank Marcus Boucher who provided very capable technical assistance for laboratory and field studies. Cory Williamson also provided substantial assistance for field projects on the Nechako River. The District of Vanderhoof has also provided substantial support for conducting white sturgeon recovery projects. In particular it allowed its waterfront park to be used as a helicopter landing site for gravel augmentation studies and as an ongoing research site.

Funding was provided by the Endangered Species Recovery Fund (World Wildlife Fund), the Interdepartmental Recovery Fund (Environment Canada), the BC Ministry of Environment and BC Hydro. All funders are thanked for their contributions which made this work possible.

On a more personal level I would like to thank my partner Anna Chase. Her continual support has allowed me to complete this project. Thanks also to Kai and Teya for being good, keep it up.

Chapter 1 Introduction

White sturgeon (*Acipenser transmontanus*) are part of an ancient lineage of 27 species within the order Acipenseriformes, which originated at least 200 MY ago (Bemis et al. 1997). Sturgeon and paddlefish are members of one of the oldest groups of extant fishes; yet despite their persistence for millions of years, nearly all species in this family are of conservation concern (Birstein 1993; Pikitch et al. 2005). Populations are declining for 19 of the 23 species for which data are available, and the fact that 63% of the species in this family are designated critically endangered by the International Union for the Conservation of Nature (IUCN) makes sturgeon one of the most endangered groups of vertebrates (Ruban and Bin Zhu 2010).

Overharvest and anthropogenic habitat changes are the most common causes of population decline, with river regulation by dams being the dominant habitat impact. The susceptibility of sturgeon to harvest and habitat change results from traits such as longevity and late maturity (Boreman 2002) in combination with their economic value as a source of food and caviar or the economic value associated with river regulation (e.g., hydroelectric power, floodplain development). The impacts of dam construction and operation have been described as one of the most dramatic and deliberate impacts of humans on the natural environment (Petts 1985; Moyle and Mount 2007). The tendency of sturgeon to reside in large rivers, which are relatively rare habitats, combined with the fact that dams affect the majority of large rivers within the Northern Hemisphere range of sturgeon (Dynesius and Nilsson 1994), makes them particularly prone to the effects of river regulation. In combination, the prevalence of anthropogenic impacts such as river regulation and overharvest make sturgeon conservation a particularly challenging objective.

White sturgeon (*Acipenser transmontanus*, Figure 1.1) is primarily a freshwater species found in the Fraser, Columbia and Sacramento rivers' watersheds. However, small populations are also present or suspected in other coastal rivers or tributaries, though they may represent transient populations (Moyle 2002; Chapman and Jones 2010). The southernmost population in the Sacramento/San Joaquin River drainage appears to be fully anadromous (Miller 1972), and populations are sufficient to support a recreational harvest fishery in San Francisco Bay (Schafter and Kohlhorst 1999). Within the Columbia River drainage most white sturgeon are trapped within the multiple impoundments that regulate the river. Both abundance and recruitment patterns vary between different impounded reaches (Coutant 2004), and in the lowermost section downstream of Bonneville Dam, populations are still sufficient to support substantial recreational and commercial harvest (JCRMS 2007).

The Fraser River is unique within the range of white sturgeon due to the absence of mainstem dams, meaning that the three populations residing in the mainstem Fraser River occupy the most pristine white sturgeon habitat available. Populations in the upper, mid and lower Fraser are estimated to contain 815 (Yarmish and Toth 2001), 3,745 (R. L. & L. 2000) and 40,000 to 120,000 individuals (over 40 cm fork length) respectively (Whitlock 2007; Nelson et al. 2010), with variation in the lower Fraser population estimates resulting from methodological differences. Most white sturgeon populations reside exclusively in freshwater within upstream areas of the Columbia and Fraser watersheds. However, populations with ocean access also use marine habitats (Miller 1972; DeVore et al. 1993; Veinott et al. 1999) and individuals are occasionally detected in marine habitats from Alaska to Baja California (McPhail 2007). Fish from all three major watersheds occupied by white sturgeon have been identified in marine waters, although it is uncertain whether marine-caught fish represent separate stocks or life history variation (Drauch-Schrier 2012; McAdam et al. unpubl.).

Although the white sturgeon is classified by the IUCN as a species of lowest concern at the species level (Duke et al. 2004), the status of different populations is highly variable (Coutant 2004). Recruitment failure was first identified in the Kootenay¹ River (Partridge 1983). In addition to the Kootenay River, populations in the Nechako and upper Columbia rivers are also undergoing chronic recruitment failure, meaning that half of the Canadian populations are affected (COSEWIC 2003). The continuation of this catastrophic impact will lead to extirpation of affected populations within one generation without successful intervention (Wood et al. 2007). While depressed recruitment has been identified for a number of sturgeon species (e.g., Dryer and Sandvol 1999; Ruban 2005; Woodland and Secor 2007), recruitment failure has been particularly well studied for white sturgeon (e.g., present study; Paragamian et al. 2005, 2009; McDonald et al. 2009). Identifying the causes of recruitment failure is challenging due to continued biological uncertainty (e.g., habitat use by larvae and age-0 juveniles) combined with the historical nature of the ecosystem impacts that affect the large rivers occupied by these populations. Because impacts to large rivers typically precede an understanding of pristine ecosystems, contemporary analyses now face the challenge of differentiating natural biological patterns from anthropogenic effects. The present investigation of white sturgeon recruitment failure clearly addresses a critical conservation need for this species, and is also expected to provide important insights into factors affecting the recruitment of other sturgeon as well as other large riverine species.

Recruitment is often determined by early life history survival (Bailey and Houde 1989), and understanding the causes of recruitment variation is a fundamental challenge in fisheries science. Multiple hypotheses have been suggested to explain recruitment variation, and the influence of a variety of factors is likely responsible both for modest recruitment variation as well as episodic very high recruitment (Anderson 1988). Although sturgeon are often described as a species with episodic

¹ The Kootenay River is referred to as the Kootenai River in the United States of America. Only the Canadian spelling is utilized in this thesis.

recruitment and occasional very strong year classes (a 'periodic' reproductive strategy; see Winemiller and Rose 1992; Pine et al. 2001), such patterns are not apparent in retrospective studies of recruitment variation (Woodland and Secor 2007; Shaw et al. 2012). In contrast to marine ecosystems, in which environmental forcing of recruitment variation may be affected by multiple independent environmental effects (e.g., wind effects, thermal effects), for riverine ecosystems the flow regime is typically considered the dominant forcing factor, and it fundamentally affects ecosystem function (Petts 1985; Bunn and Arthington 2002; Moyle and Mount 2007). Correlations between various aspects of the flow regime and recruitment have been identified for many species (e.g., Junk et al. 1989), and spring flow magnitude has been correlated with recruitment for lake sturgeon (*Acipenser fulvescens*; Nilo et al. 1997; Shaw et al. 2012) and white sturgeon (Kohlhorst 1980; Parsley and Beckman 1994).

While the relationship between sturgeon recruitment and river flow suggests that recruitment effects might be expected in response to flow regulation, the presence of recruitment failure over many years is more indicative of a regime change in the riverine ecosystem. Recruitment failure typically describes low or very low recruitment in a single year; however, for the populations examined in this study the chronic nature of recruitment failure suggests recruitment collapse is a more appropriate term.² The presence of recruitment collapse in the Nechako (Korman and Walters 2001; NWSRI 2004), UCR (UCWSRI 2002) and Kootenay (Partridge 1983; Duke et al. 1999) rivers suggests that white sturgeon populations from the upstream sections of watersheds may be more prone to severe recruitment failure. However, it is uncertain whether other species show similar patterns.

Anthropogenic impacts to rivers include loss of riparian habitats, decreased water quality and a broad suite of impacts related to river regulation by dams (Petts 1985; Moyle and Mount 2007). Floodplains are an important habitat for a variety of sturgeon species (Bemis and Kynard 2002),

² Recruitment failure is used herein to refer to the decline from a state with sustained recruitment to one without, and recruitment collapse is used to refer to the overall state of populations.

particularly for early juveniles (Bennett et al. 2005). Reductions in the availability of floodplain habitat due to diking or flow regulation lead to both the loss of habitat area (Rood and Neill 1987; Boyle et al. 1997) and decreased productivity (Snyder and Minshall 2005). The presence of elevated pollutants in many large river ecosystems leads to concerns for various sturgeon (Williot et al. 2002; Hatfield et al. 2004), and impacts have been identified both based on toxicological studies (Bennett and Farrell 1998; Feist et al. 2005; Kruse and Webb 2006; Vardy et al. 2011) and based on recruitment at the population level (Woodland and Secor 2007). However, given the presence of dams on most northern hemisphere rivers (Dynesius and Nilsson 1994) and their acknowledged impacts on sturgeon (Birstein 1993; Raspopov et al. 1994; Billard and Lecointre 2001; Pikitch et al. 2005), the most prevalent single factor affecting sturgeon habitat globally is the broad range of river regulation impacts caused by hydroelectric dams and other flow control structures. Because dams fundamentally affect both flow and sediment transport, which are the two primary influences on channel morphology, they lead to a wide range of both short- and long-term changes to the physical habitats utilized by fish, including river channel aggradation (sediment buildup) due to loss of flushing flows and decreased sediment transport capacity (Rieser et al. 1990; Ligon et al. 1995; Petts and Gurnell 2005). Large impoundments and deep hypolimnetic releases can also lead to critical downstream changes, including increased water clarity (Hildebrand et al. 1999), temperature (Clarkson and Childs 2000) and nutrient levels (Stockner et al. 2000). With regard to impacts on sturgeon, specifically identified effects include decreased connectivity (Auer 1996a; Ruban 2005), loss of riparian flooding (Coutant 2004), temperature change (Bevelheimer 2002; Paragamian and Wakinen 2002; Van Poorten and McAdam 2010) and other direct and indirect impacts of flow regulation (Votinov and Kasyanov 1978; Auer 1996b; Paragamian et al. 2001).

The importance of spawning habitat to species persistence makes it a logical starting point for the examination of recruitment effects. Although spawning locations for Eurasian sturgeon have been

identified for many years (e.g., Ruban 2005), for some species, including some white sturgeon populations, spawning locations are still uncertain. Sturgeon spawning habitat is typically described as main channel locations with high water velocity and cobble-gravel substrate (Parsley and Beckman 1994; Billard and Lecointre 2001), but descriptions are often based on spawning habitat located in dam tailraces areas (e.g., Parsley and Kappenman 2000). Notably, the first identification of white sturgeon spawning habitat in a non-regulated river (the Fraser River) identified spawning in a large side channel that was shallower and had a lower velocity (Perrin et al. 2003) than the adjacent mainstem. While spawning in dam tailraces suggests sturgeon select alternate locations when unable to access historical spawning sites, the extent to which alternate sites provide appropriate conditions is uncertain. Impacts to spawning habitat may result from altered hydraulic conditions, potentially shifting spawning to less suitable locations (McDonald et al. 2009), or due to in-stream habitat changes caused by river regulation and channel modifications (Paragamian et al. 2009; Dumont et al. 2011). This latter category of effects is addressed more extensively in Chapters 2 and 3.

Spawning adults should select appropriate habitats for progeny survival and, within a broad spawning reach, spawning locations appear to be selected based on hydraulic conditions (Paragamian and Wakinen 2002; Du et al. 2011). White sturgeon are classified as broadcast spawners, and although spawning is rarely observed, the spatially-restricted location of eggs suggests spawning occurs close to substrates. Interstitial microhabitats provide important cover at this life stage, and interstitial eggs show higher survival than eggs on the substrate surface (Johnson et al. 2006; Forsythe 2010). Additionally, inundation of eggs by even a shallow layer of fine materials causes reduced survival in white sturgeon (Kock et al. 2006). Egg development is temperature dependant, with hatching occurring between six (20°C) and 13 (11°C) days post fertilization (Wang et al. 1985). A lower temperature within the normal preference range leads to higher survival (Boucher 2012) and larger larvae (Wang et al. 1985), but low temperatures can lead to very extended times until hatch (Tiley 2006).

The larval period of fish is associated with the greatest relative mortality of any life stage (Miller et al. 1988), and yet it is typically the least understood. The strength of ensuing year classes is often set during this phase (Houde 1987; Bailey and Houde 1989), but not always (Anderson 1988). Unfortunately the use of different larval naming conventions creates confusion in the sturgeon literature. When the initiation of feeding is considered the most significant life history transition, the three phases are typically referred to as embryo – free embryo – larvae (e.g., Balon 1999). However, when hatch is considered a more important transition the three phases are generally referred to as embryo – yolk sac larvae – feeding larvae (Urho 2002). One result of these differences is that the term “larvae” is unclear, because it may refer to the one phase in the former system and two in the latter system. Use of additional terms such as eleutheroembryo (Bennett et al. 2007) and protolarvae (Zubair et al. 2012) to refer to free embryo / yolk sac larvae also contribute to this confusion, although fortunately such terms are less common. In the present study the terms embryo, yolk sac larvae, and feeding larvae are used based on the logic presented by Urho (2002), and on the consideration of hatching as the more significant life transition (Fuiman 2002).

For most sturgeon species our understanding of larval habitat use is based on laboratory studies (e.g., Kynard et al. 2002; Zhuang et al. 2003; Gessner et al. 2009); however, studies of lake sturgeon (e.g., Kempinger 1988; Auer and Baker 2002; Forsythe 2012) are notable exceptions. Drift by yolk sac larvae has been identified both in field (Howell and McLellan 2007, 2009; Braaten et al. 2008) and lab studies (e.g., Kynard et al. 2002, 2005), and a drift phase of one to six days has been suggested for white sturgeon (Brannon et al. 1985; Deng et al. 2002; Kynard and Parker 2005). While benthic hiding by lake sturgeon yolk sac larvae (Kempinger 1988; Auer and Baker 2002) suggests potential differences between species, differences in experimental methodology indicate that these differences may be artefacts of experimental conditions (see Chapters 4 and 5). This “drift or hide” dichotomy has important implications because an obligate drift phase can imply that this life phase requires

movement of larvae downstream over hundreds of kilometres of fluvial habitat (Kynard et al. 2002; Braaten et al. 2008, 2012), whereas localized hiding suggests much more spatially-restricted habitat utilization (e.g., Kempinger 1988).

While the presence of innate drift behaviour in yolk sac larvae is uncertain, drift by feeding larvae is widely identified in association with the initiation of feeding. High larval mortality during the first feeding period (Anderson 1988) typically results from the combined effects of starvation and predation. While there is a complex relationship between larval size and vulnerability to predation (Fuiman 1994; Lundvill et al. 1999), rapid larval growth is considered an adaptation to limit mortality during this phase. In captivity white sturgeon larvae can reach 27-38 mm and 107-287 mg at 46 days post hatch (dph) from starting lengths and weights of 14 mm and 23 mg at 1 dph (Boucher 2012). Additionally, substrate conditions experienced by yolk sac larvae influence subsequent growth of feeding larvae. Growth and survival are also affected by temperature, with optimum growth at 15 °C for white sturgeon (Wang et al. 1985); however, lower temperatures (13.5 °C) lead to increased survival in the presence of gravel substrate (Boucher 2012).

The fact that feeding larvae and early young of year fish are widely dispersed in large rivers makes them challenging to study, and habitat use by these phases is poorly understood. Wild caught young of the year reach lengths of 220 mm after their first season of growth (McCabe and Tracy 1994), which again emphasizes the rapidity of early growth. The survival of hatchery-produced white sturgeon when released at the age of ten months (Golder 2006b) indicates that recruitment levels are determined prior to that age in the upper Columbia River. Correlations between year class strength and environmental conditions during the egg and larval period suggest that recruitment is set during early life history (Nilo et al. 1997). In lake sturgeon, increased recruitment in response to restoration of spawning habitat (Kerr et al. 2010) suggests that recruitment is strongly influenced by survival prior to

drift; however, the lack of correlation between larval drift abundance and subsequent recruitment suggests recruitment may be determined after feeding larvae drift (Dumont et al. 2011).

It is widely acknowledged that investigations of recruitment failure are limited by our understanding of biological factors such as habitat use during early life history, but what often goes unstated is the inherent difficulty of investigating fish recruitment in a large river environment. Large river habitats are notoriously hard to study (Johnson et al. 1995). Although juveniles and adults can be easily sampled, the actual habitats they occupy are often difficult to describe (e.g., spawning locations). This difficulty is even more relevant for the smallest life stages because differences in the physical scale of eggs or larvae and their large river habitats create a proverbial 'needle in the haystack' problem. Additionally, limited studies from pristine habitats mean that the *in situ* understanding of many species, including white sturgeon, is primarily derived from highly-altered habitats. Differentiating between innate biology and the effects of habitat alteration adds additional complexity. For example, captures of drifting yolk sac larvae (Golder 2005a, 2006a, 2010; Howell and McLellan 2009) have led to a strong focus on drift behaviour (e.g., Braaten et al. 2008). However, the presence of hiding by lake sturgeon (Kempinger 1988; Auer and Baker 2002) and Atlantic sturgeon (*A. oxyrinchus*; Gessner et al. 2009) suggests a more comprehensive understanding of larval habitat is required. Because recruitment failure is often considered a result of increased early life history mortality, understanding how habitat conditions affect early life history survival may be fundamental to understanding recruitment failure.

In addition to biological uncertainty, retrospective evaluations of ecological changes are often complex, and the ability to prove causation retrospectively is limited (Fabricius and De'ath 2004; Suter 2007). Uncertainty regarding the relative importance of impacts may therefore explain why investigations of sturgeon population declines often present an unranked list of potential threats (e.g., Williot et al. 2002; Hatfield et al. 2004). While many factors can have negative effects, the challenge is

determining which threats are fundamental (e.g., overfishing, recruitment failure) and which might be tolerable, though undesirable. The fact that a single impact category (e.g., effects of dams) can affect multiple impact mechanisms, and only some of those changes may be detrimental, further complicates the analysis.

The present study of white sturgeon recruitment failure combines the diagnosis of likely causes (based on an examination of historical recruitment patterns) with both laboratory and field enclosure studies that examine the role of substrate condition on larvae, with a focus on yolk sac larvae. Diagnosis of recruitment declines was based on retrospective comparisons of recruitment and environmental change for white sturgeon populations in the Nechako (Chapter 2) and upper Columbia rivers (Chapter 3). The outcomes of these two diagnostic analyses provided the basis for laboratory (Chapter 4) and field (Chapter 5) studies that evaluate the effects of substrate on larval behaviour and survival.

The Nechako River case study provides the simplest example of recruitment failure because the watershed is affected by a single dam, and other large-scale anthropogenic impacts to the river are limited. The presence of a distinct white sturgeon population in the Nechako River has now been identified based on movement patterns (R. L. & L. 2000), mitochondrial DNA (Smith et al. 2002) and nuclear microsatellites (Drauch Schrier 2011), but the population estimate in 1999 was only 571 (95% CI = 421-890) individuals (R. L. & L. 2000). Recruitment failure was identified based on the absence of juvenile age classes, and led to a preliminary assessment of potential causes of recruitment failure (Korman and Walters 2001) and the initiation of recovery planning in 2000 (NWSRI 2004). Spawning was identified in a relatively shallow braided river reach near Vanderhoof in 2004 based on telemetry, direct observation of pre-spawning behaviour and the capture of viable eggs (Liebe et al. 2004). Spawning has subsequently been studied in this reach nearly annually. Eggs are routinely captured at three main locations within the 2 km spawning reach, and drifting yolk sac larvae are occasionally

captured (Triton Environmental Consultants 2009). Habitat conditions in the spawning reach have changed according to discussions with long-term residents of the area, suggesting that changes in spawning habitat quality may have affected egg or larval survival.

Understanding factors that influence recruitment and the causes of recruitment variation is a fundamental question in fisheries science, but analyses of recruitment-environment relationships have been criticized for reasons such as the transient nature of correlations (Myers 1998). However, the present approach, which uses the present age structure to ‘hindcast’ past recruitment using virtual population analysis (Hilborn and Walters 1992), is focused on the timing of drastic recruitment declines and should limit concerns about longer-term evaluations of recruitment variation (e.g., Catalano et al. 2009). In the Nechako River case study, recruitment decline timing is compared to the timing of the completion of Kenney Dam (and the formation of Knewstubb Reservoir) and river diversion structures in 1952, as well as subsequent flow changes and associated habitat effects. Aside from river regulation, other anthropogenic changes to the Nechako River are limited. However, avulsions (i.e., shifts in the river channel) of the Cheslatta River in 1961 and 1972 at its confluence with the Nechako River³ may also have affected downstream habitats; therefore, I also investigated the potential relationship between recruitment failure and habitat changes subsequent to the Cheslatta avulsions. Historical habitat changes were identified based on historical air photos and retrospective analysis of river bed elevation. Temporal patterns for identified habitat changes were then compared with hindcasted recruitment to identify potential links between habitat change and recruitment failure.

Diagnosing causes of recruitment decline in the upper Columbia River (Chapter 3) is more difficult due to the greater variety of environmental impacts and greater biological complexity, and in particular because both impacts and biological responses show spatial and temporal variation. Upper

³ The spillway associated with Knewstubb Reservoir is located 75 km northwest of Kenney Dam and drains into the Cheslatta River watershed. As a result, flow in the Cheslatta River is artificially increased.

Columbia River white sturgeon have been intensively studied since the early 1990s, and population estimates for the Canadian and American portions of the reach are 1,157 (95% CI = 414-1900; Irvine et al. 2007) and 2,037 (95% CI = 1093-3223; Howell and McLellan 2007) respectively. Additionally, 52 fish (95% CI = 37-92) reside in Arrow Lakes Reservoir (Golder 2006d). Recruitment failure was identified in the early 1990s based on shifts in size composition relative to sampling in the 1980s (Irvine et al. 2007). A spawning site downstream of Waneta Dam was identified in 1993 with three additional spawning sites now detected in British Columbia and two detected in Washington State (Howell and McLellan 2009). The identification of yolk sac larvae as the oldest developmental stage regularly detected at most spawning sites, and detection of feeding larvae (but not early juveniles) at one site suggest that early life history survival is a key recruitment bottleneck for this population.

The broad range of anthropogenic changes to the upper Columbia River complicates the identification of specific impacts and their timing relative to the simpler case of a single dam on the Nechako River. White sturgeon in the upper Columbia River are potentially affected by over 15 dams within the principal influent watersheds of the Columbia, Kootenay and Pend d'Oreille rivers. While large storage reservoirs impounded by Hugh Keenleyside Dam (completed 1968) and Mica (1974) have led to substantial changes in the upper Columbia River hydrograph, impacts on temperature (Hamblin and McAdam 2003; Tiley 2006), hydraulic conditions (Fissel and Jiang 2007; Northwest Hydraulics 2007) and dissolved gas supersaturation (or elevated total gas pressure, TGP) (R. L. & L. 1995; CRIEMP 2005, 2008) also result from both mainstem and tributary dams. In addition, the presence of industrial activity, including a pulp mill at Castlegar (since 1961) and a lead zinc smelter at Trail (since 1910), affect water quality due to the release of liquid effluents and historical releases of metallurgical slag (CRIEMP 2008). While a variety of impacts to biotic and abiotic ecosystem components have been identified in the upper Columbia River, identifying the specific origin and timing of impacts, as well as their potential relationship to white sturgeon recruitment, presents a substantial challenge.

Genetic evidence suggests the presence population structure and spatial heterogeneity in habitat use (Nelson and McAdam 2012), which together provide additional complexity and important contrast in the upper Columbia River case. Four high-use habitat areas have been identified (R. L. & L. 2001; Howell and McLellan 2007), and individuals show high fidelity to particular habitats based on analysis of growth (van Poorten and McAdam 2010), fin ray chemistry (Clarke et al. 2011) and movement and genetics (Nelson and McAdam 2012). These groups likely represent historical stock structure within the unimpounded upper Columbia River, and their historically-derived differences continue to lead to spatial heterogeneity under modified habitat conditions of the regulated river. Recruitment differences between stocks have been widely used to examine causes of recruitment variation (Myers et al. 1997; Manderson 2008). However, because populations occupying similar habitats should show similar demographics (Moran 1953), stock structure for the upper Columbia River provides the opportunity to use stock-specific recruitment histories to evaluate causes of recruitment decline. Similar to Chapter 2, hindcasted recruitment formed the basis of analysis. However, evaluation of the upper Columbia River case also included the consideration of three aging accuracy scenarios (no inaccuracy, low inaccuracy, high inaccuracy) to evaluate the potential effects of aging inaccuracy on recruitment decline timing and apparent causation. In addition to comparing recruitment decline timing with the timing of major anthropogenic changes in the watershed, the evaluation was primarily based on a weight-of-evidence evaluation of eleven recruitment failure hypotheses using ecoepidemiological approaches (Forbes and Callow 2002; Suter 2007). While structured evaluations to identify potential causation are well developed in the field of epidemiologically, there are relatively few uses of such methods in the field of fisheries (see Breyers 1998; Lowell et al. 2000; Fabricius and De'ath 2004). Although multiple environmental changes are present in the upper Columbia River watershed, the present method provides a fairly simple heuristic approach for the identification of potential causes of recruitment failure.

The evaluation of recruitment failure causation in the Nechako River (Chapter 2) and upper Columbia River (Chapter 3) supports the hypothesis that recruitment failure results from decreased early life history survival due to increase fine substrates at spawning sites. The need to validate this apparent relationship therefore led to the investigation of the effects of substrate condition on yolksac larvae habitat use and survival in Chapter 4. Elevated mortality at the egg stage has been identified in the Kootenay River based on the lack of larval captures and the rapid inundation of egg mats with sediment in the spawning reach (Duke et al. 1999; Paragamian et al. 2001). Laboratory investigations have also shown elevated mortality when eggs are covered by as little as 5 mm of sand (Koch et al. 2006). However, the regular detection of yolksac larvae in the Nechako and Columbia rivers indicates survival beyond the egg stage. Identification of the substrate preference of yolksac larvae, but not feeding larvae (Bennett et al. 2007), suggests that substrate changes may have a greater effect on yolksac larvae; however, behaviour and habitat use during this stage are uncertain. Review of investigations of larval behaviour for 14 sturgeon species identified differences in findings and methodology, and some critical limitations (Table 1.1). For example, a maximum of three females supplied the progeny for each of the eleven studies that identified parental numbers, and five of those studies (Kynard et al. 2003; Zhuang et al. 2003; Kynard and Parker 2005, 2010; Gessner et al. 2009) utilized progeny from a single female. Most studies also decreased replication by mixing progeny when different crosses were used, and by conducting tests in a single tank. However, the most serious limitation in many prior studies is that substrate conditions were not representative of natural habitat (see Table 1.1). Surprisingly, limitations in prior laboratory studies are not widely recognized (though see Gessner et al. 2009), and laboratory studies are readily considered representative of the species' behaviour under natural conditions. The possibility that prior studies have biased our understanding of early life history behaviour is therefore examined in Chapter 4.

The laboratory investigations reported here examined five different substrate conditions representing substrate sizes from sand to cobble, as well as embedded cobble. Additionally, progeny were derived from multiple crosses over two years to limit family effects. Evaluations were based on observations of larval behaviour during exposure to substrates in a flume tank, with quantification based on the number of larvae that either hid or drifted in response to different substrates. In addition, the duration of drift was estimated based on hiding locations. The effect of substrate condition on larval survival was also evaluated to provide a direct link to potential recruitment effects. The results of these investigations identify important limitations of the methodologies used in prior studies. They also provide a more comprehensive understanding of habitat use by yolksac larvae, as well as further evidence that substrate alteration at spawning sites in the Nechako and upper Columbia rivers is the primary cause of recruitment failure.

The final portion of this study evaluated larval responses to substrate conditions *in situ* to examine the potential for substrate modification to increase yolksac larvae survival under natural conditions within the Nechako River. While laboratory findings indicate that substrate affects drift behaviour and survival, laboratory studies cannot fully reproduce conditions in riverine habitats. For example, prior studies of yolksac larvae all had minimum water velocities of less than 5 cm/sec (Table 1.1). Although the present laboratory studies examined water velocities of 4 and 20 cm/sec these are still much lower than velocities commonly experienced at spawning sites (i.e., > 1 m/sec; (Parsley and Beckman 1994). The inclusion of benthic sampling also allowed evaluation of larval condition and survival throughout the yolksac larvae stage; *in situ* survival of yolksac larvae has previously only been estimated by Johnson et al. (2006) and Forsythe (2010). Field testing of laboratory findings is an important step toward ensuring the reproducibility of laboratory findings under more complex conditions. Field-based verification is also particularly important due to the high cost of habitat

remediation (e.g., flow restoration), and may have important implications for the spatial extent and cost of restoration as well as how it is conducted.

The set of studies in this thesis provide a progression from using presently available data to diagnose potential causes of recruitment failure to experimental analysis of how substrate condition affects larval behaviour, survival and potentially recruitment. The initial diagnostic phase in Chapters 2 and 3 provides a scientifically credible approach to identify habitat changes that most likely caused recruitment to collapse in both the Nechako and upper Columbia rivers. In contrast with most prior studies, the laboratory analysis of the effects of various substrates on yolk sac larvae (Chapter 4) provides a more unified understanding of the importance of substrate and clarifies a number of discrepancies resulting from methodological differences between prior studies. The extension of these findings to *in situ* manipulative habitat experiments in the Nechako River demonstrates the survival benefits of restored substrates under natural (but not pristine) conditions, and therefore provides the basis for larger restoration works. Collectively, the research I completed for this thesis should help to diminish biological uncertainty regarding the early life history of sturgeon, and more specifically, the probable causes of recruitment failure. In doing so, my hope is that it will aid the prevention of further impacts and support future habitat restoration for the conservation of wild populations.



Figure 1.1 White sturgeon *Acipenser transmontanus*. Drawing by Loucas Raptis based on a fish from the Nechako River. © BC Ministry of Environment, by permission.

Table 1.1 Summary of studies evaluating behaviour of sturgeon yolksac larvae. Only studies that provided data for the indicated criteria are included. For parentage, the number of parents (F=females, M=males) and whether progeny were mixed are indicated. NS=not stated, NA=not applicable.

Species	Parentage	Substrate (diameter/type, configuration)	Water velocity (cm/sec)	Drift by yolksac larvae Yes/No/Low, duration	Reference
Amur sturgeon	3F/3M (mixed)	5-6 cm, 10 piles	3-10.5	Y, 0- 2 dph	Zhuang et al. 2003
Atlantic sturgeon	NS (500 eggs)	gravel, 30 cm ²	5-9	N	Kynard and Horgan 2002
Atlantic sturgeon	1F/2M	NS	NS, likely low	gravel=N, sand=Y	Gessner et al. 2009
Chinese sturgeon	2F/3M (mixed)	5-6 cm, 10 piles	2.8-10.6	Y, 1-7 dph Low 8-30 dph	Zhuang et al. 2002
dabry's sturgeon	1F/1M	5-6 cm, 10 piles	2.8-10.6	Low	Kynard et al. 2003
green sturgeon	1F/2M or 2F/4M	10-15 cm, 6 rocks	1-9	N/Low, 0-10 dph	Kynard et al. 2005
Gulf sturgeon	NS (200 eggs)	5 cm, NA	1-9 cm/sec	Low,	Kynard and Parker 2004
kaluga	1F/2M (mixed)	5-6 cm, 10 piles	3-10.5 cm/sec	Y, 0-3 dph	Zhuang et al. 2003
pallid sturgeon	NS	5 cm, NA	3-9 cm/sec	Y, 0-8 dph	Kynard et al. 2002a
Russian sturgeon	3F/3M (mixed)	5-6 cm, 10 piles	2.8-10.6 cm/sec	Y, 0-6 dph	Kynard et al. 2002b
shortnose sturgeon	3F/9M (mixed)	Astroturf	NS	NS	Richmond and Kynard 1995
shovelnose sturgeon	NS	5 cm, NA	3-9 cm/sec	Y, 0-8 dph	Kynard et al. 2002a
Siberian sturgeon	NS	concave metal sheet	NS	Y, 0-3 dph	Gisbert et al. 1999
white sturgeon	NS	Various	NS	Y, 5 hrs or 0-1 dph	Brannon et al. 1983, 1985
white sturgeon	1F/1M	10-15 cm, 6 rocks	1-9	Low, 3 - 6 dph	Kynard and Parker 2005
white sturgeon	1F/1M	10-15 cm, 6 rocks	3-9 cm/sec	Low, 0-7; 9-12 dph N, 8 dph	Kynard and Parker 2010

Chapter 2 - Linkages between white sturgeon (*Acipenser transmontanus*) recruitment and altered bed substrates in the Nechako River, Canada

Introduction

Flow regulation and floodplain abstraction are common impacts associated with river regulation, and sturgeon are widely affected by this and other anthropogenic effects to rivers (Birstein 1993; Coutant 2004; Paragamian et al. 2005). For white sturgeon populations in the Nechako, upper Columbia and Kootenay rivers such impacts have led to nearly complete recruitment collapse, resulting in the classification of this species as endangered in Canada (COSEWIC 2003). While river regulation is implicated as an apparent cause, the mechanisms of recruitment failure have not been completely described. As a result, biological uncertainty continues to limit restoration. White sturgeon share many life history attributes with other flood spawning species, which may make them particularly prone to the effects of river regulation. They are highly fecund non-annual spawners that typically spawn after the spring-summer freshet peak. Spawning sites are most often found in turbulent or turbid river reaches upstream of floodplains (Coutant 2004; Bemis and Kynard 2002). For white sturgeon and other sturgeon species, historical floodplains are typically unavailable or are severely diminished, and dams may block access to historical spawning sites (e.g., Ruban 2005; Wang and Xia 2009).

Identification of the causes of past ecological changes presents a substantial challenge due to the variety of factors that affect large rivers, and the fact that suitable environmental data are often unavailable (Suter 2007). In the present case, biological uncertainty, and particularly habitat use during early life history, also limits the identification of potential habitat changes that affect early survival. In

response to such limitations, Gregory and Long (2008) based their evaluation of recruitment failure in the upper Columbia River on professional judgment, but showed only limited differentiation between four of five hypotheses.⁴ Based on a range-wide examination of white sturgeon recruitment, Coutant (2004) suggested that a lack of newly-wetted vegetation, and its provision of egg adhesion sites and physical cover for larvae, is a broadly applicable hypothesis for recruitment failure. However, because recruitment collapse of the Nechako River population was not examined in Coutant (2004), the present analysis provides an independent test of Coutant's (2004) hypothesis.

While understanding the causes of recruitment declines is fundamental to species recovery, recovery programs often lack of a clear diagnostic approach by which population data are used to evaluate causes of population declines. As a result, recovery planning documents often contain an extensive list of potential impacts without a means to evaluate their relative importance (e.g., Williot et al. 2002; Hatfield et al. 2004; Wildhaber et al. 2011; Zhang et al. 2011). Investigating the causes of recruitment failure also presents a challenging problem because it couples high biological uncertainty with the high costs of restorative action, such as flow restoration. Diagnostic analysis using presently available information therefore provides a valuable approach because it allows evaluation of potential recruitment failure mechanisms and prioritization of restoration options. While the historical nature of recruitment declines makes analysis challenging, white sturgeon are not unique in this regard. Perry et al. (2004) outlined six general approaches including experimentation, modelling and evaluating the timing of declines. The approach described as multiple competing hypotheses (based on Caughley 1994) is also similar to the ecoepidemiological approach used in Chapter 3 (see Suter 2007).

⁴ The supported hypotheses were geomorphological effects, changes to flow and turbidity, changes in the fish community and changes in nutrients and food supply. The unsupported hypothesis addressed contaminant effects.

The approach taken used virtual population analysis (Hilborn and Walters 1992) to hindcast recruitment followed by the identification of temporally correlated habitat changes (i.e., the timing of decline approach of Peery et al. 2004). Similar to the evaluation of recruitment residuals (e.g., Maceina 2003; Shaw et al. 2012), evaluation of a hindcasted recruitment index assumes that recruitment residuals reflect environmental effects (e.g., Quist 2007, Catalano et al. 2009). However, the focus of the present analysis is on the timing of drastic recruitment declines at the initiation of recruitment collapse, rather than the full recruitment time series. While the longevity of sturgeon may make them particularly amenable to this type of analysis, aging error, particularly in older fish, can limit the utility of evaluations based on year class strength (Bradford 1991; Rien and Beamesderfer 1994); however, despite this concern the presence of severe recruitment declines should be detectible. While aging imprecision may smooth decline patterns, it should neither eliminate them nor change their apparent timing. By contrast, inaccurate age determinations may have a strong and fundamental effect, and the possibility of aging inaccuracy is considered in the present analysis.

White sturgeon in the Nechako River have been recognized as a population distinct from those in the mainstem Fraser River based on spatial differences in habitat use (R. L. & L. 2000), genetic analysis (Smith et al. 2002; Drauch-Schrier 2012) and demographic differences (Korman and Walters 2001). A population of 571 fish (CI = 421-890) was identified during a basin-wide study between 1995 and 1999 (R. L. & L. 2000), and recruitment failure was suggested due to extremely low juvenile abundance. Evaluation of population status and early development of recruitment failure hypotheses were presented by Korman and Walters (2001). Recruitment failure hypotheses were further developed within the population-specific recovery plan (NRWSRP 2004), including the hypothesized effect of altered river bed substrates addressed in this analysis.

Flow manipulation and associated effects are the only major developments in the Nechako River that likely affect white sturgeon spawning and recruitment, resulting in a relatively simple case study. The river was impounded by the Kenney Dam in 1952, and 59% of the mean annual discharge (as measured at Vanderhoof due to limited historical data above the Nautley River confluence) is diverted westward through diversion tunnels to a powerhouse located near the coastal community of Kemano. The general changes to the Nechako River hydrograph therefore include a substantial decrease in mean annual flow as well as a diminished frequency and magnitude of high flow conditions. Additionally, downstream flows into the Nechako River are controlled at the Skins Lake Spillway (about 75 km north-east of Kenney Dam), which discharges into the Cheslatta River watershed. One impact of substantially increasing the Cheslatta River flows was an increase in the sediment supply to the upper Nechako River, including the introduction of about 1,000,000 m³ of sand, silt and fine gravel due to the 1961 and 1972 avulsions (shifts in the river channel) at the confluence of the Cheslatta and Nechako rivers (Hay and Company 2000). While the impacts of river regulation have been substantial – for example, with respect to physical habitat (e.g., loss of side channels, see Rood and Neil 1987) and temperature (MacDonald et al. 2007) – the river channel is affected by relatively few other anthropogenic effects (e.g., dykes are absent). As a result, the Nechako River case study provides a relative simple evaluation compared to the upper Columbia River (Chapter 3) and the Kootenay River (Paragamian et al. 2005, 2009; McDonald et al. 2010). The near absence of harvest in this population also allows the analysis to be restricted to river regulation effects rather than the combination of harvest and river habitat degradation, which affect many other sturgeon populations.

In order to examine habitat changes in the Nechako River that potentially contribute to white sturgeon recruitment failure, the present analysis used a hindcasted recruitment index to identify the timing of a severe recruitment decline, and used spatial and temporal patterns of identified environmental changes to evaluate potential habitat-based mechanisms of recruitment failure. The

possibility that recruitment failure results from the absence of floodplain inundation due to river regulation (Coutant 2004) was tested by comparing the timing of recruitment declines in the Nechako River to when flow regulation affected riparian flooding. Additionally, temporal and spatial patterns in the loss of side channel habitat were compared to recruitment decline patterns to evaluate whether recruitment failure represents a response to changes to off-channel or mainstem habitats. The temporal similarity between the timing of the recruitment decline and identified habitat changes also led to a specific focus on apparent changes to riverbed substrates in the white sturgeon spawning habitat located at Vanderhoof, BC. In combination, the limited set of anthropogenic factors affecting the population, the lag between dam completion and recruitment failure, and the rapidity of this failure were all identified as useful attributes for recruitment failure diagnosis.

Methods

Recruitment reconstruction

A recruitment time series was estimated using age composition data collected during a 1995 to 1999 study of white sturgeon in the Nechako River watershed (see R. L. & L. 2000). Fish from the Nechako River were primarily (93%) captured using set lines. Set lines are thought to representatively sample relative abundances of fish over a wide range of ages, from 15 upward (Elliot and Beamesderfer 1990). Because the scarce young (age 10-20) fish included in the calculation (and leading to low recruitment estimates) were common when sampled with the same gear in 1982 (Dixon 1986), there is no reason to suspect that younger fish are underrepresented in the sample due to gear bias. Age estimates from annuli counts on fin ray cross sections were derived by at least two experienced readers. Due to the importance of age validation, age distributions from Dixon (1982) and R. L. & L. (2000) were compared as a means to examine aging bias after correction for gear type and capture year.

Apparent relative recruitment R_t for years t prior to the age sampling was back calculated using the equation:

$$R_{t-a} = P_a * e^{a*M}$$

where $P(a)$ is the proportion of the sample fish that were age “ a ” at $t=1995$. A natural mortality rate of $M=0.08/\text{year}$ was assumed based upon analysis of catch curves and tagging studies reviewed in Korman and Walters (2001). The key assumption in this method, besides the sample proportions of fish at age being representative of the age composition of the remaining extant population, is that natural mortality rate M has been stable over time. Also, including higher M for younger ages (as seen in tagging data, e.g., Ireland et al. 2002) would not change the index pattern at all except to scale it upward in absolute magnitude, as no such younger fish were included directly in the estimation via nonzero p_{age} values.

Hydrograph alterations

Flow data were extracted from the HYDAT database of the Water Survey of Canada (WSC). Due to the limited flow data for the upper Nechako River, flows upstream of the Nautley confluence were estimated by subtracting Nautley River flow (Gauge 08JA001) from Nechako River flow at Vanderhoof (Gauge 08JC001). Any errors caused by this method are considered to be minor relative to the effects of river regulation.

Geomorphological analysis

Analysis of geomorphic change was achieved through examining a time series of air photos that were available for 13 different years between 1928 and 1995 (see Table 2.1). Four habitat clusters were identified using air photos taken from May to June 1978 (Figure 2.1). Each cluster contained at least one putative spawning site, identified as a chute or rapid where water velocities were likely be elevated under flood conditions (e.g., S1a=spawning site a in cluster #1). Potential spawning sites also

had to be located upstream of a putative rearing site (e.g., R3b=rearing site b in cluster 3), identified as an area with increased riparian habitat, such as a flanking floodplain. Within each habitat cluster, analysis focused on changes at the putative spawning and rearing habitat units based upon air photos covering both the pre- and post-regulation period (i.e., pre- and post-1952). Substrate characteristics were also observed (e.g., with respect to grain size and embeddedness) during an October 2002 field reconnaissance to ground truth observations based on air photo analysis.

Evaluation of river bed elevation changes in the vicinity of the white sturgeon spawning reach by specific gauge analysis used the rating tables for the Water Survey of Canada gauge site at Vanderhoof (08JC001) for the period 1949 to 2002. The specific flows analyzed were 113, 227, and 340 m³/sec. Temporal changes in water-level gauge height at specific flows indicate changes in channel bed elevation.

Results

Recruitment reconstruction

Comparison of aging results from Dixon (1986) (n=20 fish) and R. L. & L. (2000) (n= 165 fish) used standardized capture years of 1980 and 1995 respectively, and considered only fish caught using set lines. After these standardizations, the modal age shows a difference of 16 years between studies (Figure 2.2).

Poor representation of fish less than 15 years old, due possibly to gear selectivity and limited abundance of fish greater than 50 years old, made recruitment reconstruction most accurate for the period 15 to 50 years prior to the mean capture year (1996). Therefore, analysis of the recruitment time series begins in the year 1946. The general pattern of projected recruitment indicates variable recruitment from 1946 to 1964 (Figure 2.3). The rapid decline in recruitment may have begun in 1964,

though recruitment until 1966 is still within the pre-1964 range. The most definite recruitment decline occurred in 1967, and subsequent recruitment remained very low with only minor variation.

Hydrograph alterations

Since the completion of Kenney Dam in 1952, there have been marked declines in total annual flow volume due to diversion of water out of the basin, and freshet flows have decreased (Figure 2.4). The reservoir filling period is notable for causing extremely low flows between 1953 and 1956. Subsequent to this period, until 1978, releases to the Nechako River were more variable during the freshet period, with the average annual peak discharge reduced to approximately half of the pre-regulation value. A more uniform release strategy comprised of low flows through the former spring freshet period and moderate flows in the summer was adopted in 1981 (Figure 2.4). Subsequent to 1981 and until 2007, the only year with a high spring freshet flow event was 1997.

Geomorphological analysis

A historical series of air photos was used to evaluate substrate changes to putative sturgeon habitat and to assess the timing of apparent changes due to the downstream movement of substrates subsequent to the Cheslatta avulsions. Unfortunately, variation in photo quality and the need to compare air photos at similar discharge levels limited the comparisons to the years indicated in Table 2.1. The identification of fine sediment accumulation at putative spawning and rearing sites indicates accumulation throughout the upper river. Due to the comparability of multiple photos, 1966 to 1973 can be clearly identified as a period of sediment accumulation for site R2b. Substrate accumulations at site R3a, immediately downstream of the Vanderhoof spawning site (Table 2), occurred between 1953 and 1973. However, the lack of accumulation at site R2b between 1960 and 1966 suggests that sediment accumulation at site R3b most likely occurred after 1966. These comparisons indicate substrate accumulations indicative of downstream movements of Cheslatta avulsion materials that

arrived at the Vanderhoof white sturgeon spawning site between 1966 and 1973. Accumulations noted for site R4 in 1966 had a notably different composition, and appear to be an effect of localized down cutting at the mouth of the Cluculz Creek rather than an accumulation of Cheslatta avulsion material. For other sites, the timing of accumulation cannot be defined more precisely than 1953 to 1985 due to limited air photo availability.

Specific gauge analysis for the Vanderhoof water survey site indicates relatively stable conditions from the period of dam completion until 1970, when a period of aggradation began (Figure 2.5). The most significant aggradation occurred between 1975 and 1995, and another period of degradation began in 1996. In addition, the technical notes in the Water Survey of Canada records for this site indicate large accumulations of sand and gravel in 1972 and 1976 (records provided by Lynn Campo, Water Survey of Canada).

Changes to the Nechako River hydrograph and changes to river bed substrates at the Vanderhoof white sturgeon spawning site represent the two principal environmental changes identified that may affect white sturgeon recruitment. The 15 year lag between the initiation of flow regulation and recruitment failure suggests flow changes provide an unlikely explanation for recruitment failure. The lack of a direct effect of flow, or other closely correlated changes, is further emphasized by the lack of recruitment restoration in response to subsequent high flow events. In contrast, the initiation of recruitment failure occurs within the 1966 to 1973 period of habitat change identified based on air photo analysis. Although river bed aggradation apparently began three years after the recruitment decline (in 1970) this difference is potentially explained by the incorporation of fine substrates within the previously gravel substrate of the spawning reach (i.e. increased embeddedness) prior to the onset of aggradation, and due to the location of the WSC site at the downstream end of the spawning reach.

Discussion

The temporal similarity of substrate changes in the Nechako River at Vanderhoof and the initiation of recruitment failure suggest that substrate conditions in white sturgeon spawning habitats may play an important causal role in recruitment failure. The identification of potential links between habitat change and recruitment failure also indicates the utility of using hindcasted recruitment as part of retrospective evaluations of habitat change. The Nechako case study provides a relatively simple application of this approach because the river is affected by a single dam, and additional large-scale anthropogenic effects are limited (e.g., dykes are absent). In conjunction with other studies that also identified impacts of substrate changes on sturgeon (Nichols et al. 2003; Paragamian et al. 2009; Du et al. 2011), these results suggest that substrate change at spawning sites may be common across multiple sturgeon species. Further consideration of recruitment decline patterns also provides a more detailed understanding of the potential biological mechanisms, and suggests that recruitment failure appears to be the result of spatially localized changes to spawning habitat rather than impacts to off-channel habitats or larger-scale whole river effects.

Unbiased age estimation is critical for recruitment reconstruction, and errors may be incurred due to capture methods or inaccurate age estimation. Fish used for age estimation were primarily (93%) captured using set lines. While set lines are biased toward larger fish, they apparently have little bias for fish above the size reached at about age 15 (Elliot and Beamesderfer 1990). This sampling method should therefore have little effect on the present analysis as it focuses on events more than 15 years prior to the mean capture year, and very few fish (6 of 170) younger than age 15 were included in the analysis.

While full age validation has not been achieved for white sturgeon, comparison of the aging results from Dixon (1982) and R. L. & L. (2000) provides a preliminary means of validation. The

similarity between shifts in modal age of 16 years and the interstudy interval of 15 years is an indication of annual annulus formation at least for fish up to age 30 (the modal age of fish from R. L. & L. 2000). Based on the difference between the mean capture year (1996) and the timing of recruitment failure (1967), fish about aged 29 years were the primary determinants of recruitment failure timing, and therefore estimates of recruitment decline timing may be minimally affected by aging inaccuracy. While this comparison alone does not provide full age validation (Campana 2001), it does indicate that the aging bias suggested by Paragamian and Beamesderfer (2003) leads to overestimation of aging error effects for Nechako River white sturgeon less than about age 30 years. A similar inference is made by Veinott and Evans (1999) for fish from the lower Columbia River. Analysis based on upper Columbia River white sturgeon also indicates that the aging error identified by Paragamian and Beamesderfer (2003) may be overestimated (Chapter 3); Golder (2005b) also suggests the high level of underaging proposed by Paragamian and Beamesderfer (2003) may be biased due to their methodology. As a result of the above findings, the present analysis was pursued with the assumption that age estimates were accurate. While aging imprecision would also affect this analysis (Rien and Beamesderfer 1994), its effect should be minimal because imprecision would generally dampen variation, but not alter the timing of the marked changes, such as the drastic recruitment declines in 1967.

Regulation of Nechako River flows began in 1952 with the completion of Kenney Dam, and the following three years had very low flows due to reservoir filling requirements (Figure 2.4). Subsequently, total annual river flow was still markedly lower than pre-regulation due to significant out of basin water diversions. However, flows during the period 1957 to 1977 remained quite variable, and both high-discharge freshets and low winter flows occurred on occasion throughout this period. A further marked and consistent decline in freshet volume began in 1978 (Figure 2.4) and was continued with the 1981 adoption of a new flow regime, which balanced even-greater flow diversions with

moderate summer flow releases for the protection of anadromous salmonids (see MacDonald et al. 2007).

The rapid recruitment decline in 1967 occurred 15 years after the initiation of flow manipulation. The absence of a more immediate recruitment response to flow alterations, or in conjunction with the second major reduction in freshet volume in 1978, indicates the recruitment failure is not a direct effect of flow alteration (i.e., changes in hydraulic conditions or lost access to spawning sites). Although the degree of hydrograph alterations has been variable since impoundment, the greatest effect on the flows was during the three initial years of reservoir filling. Yet recruitment persisted during this period. In addition, there was no apparent recruitment signal due to freshet flows of historical magnitude in 1976. Taken together, these findings indicate that by themselves, hydrograph alterations do not provide a simple uni-causal explanation for the observed recruitment failure of the Nechako River population.

The only other major perturbation to this watershed between 1952 and 1967 was an avulsion into the upper Nechako River near Cheslatta Falls in August 1961 (Hay and Company 2000). This event was one of two avulsions caused by channel shifts in the Cheslatta River near its confluence with the Nechako River (the second was in July 1972) that collectively added 1,000,000 m³ of silt, sand and fine gravel to the river channel; about half of this material was subsequently moved downstream (Rood and Neill 1987). Tracking the downstream sediment movements using air photos is challenging due to the availability of suitable quality photos at the required flows. However, multiple photos of site R2b identify sediment accumulation between 1966 and 1973, indicating that Cheslatta avulsion sediments arrived upstream of the Vanderhoof spawning site between 1966 and 1973. The identification of sediment accumulation in those years suggests that recruitment failure was coincident with changes in substrate conditions in the vicinity of the Vanderhoof spawning site. While results based on air photos

are not as definitive as the specific gauge analysis, they may provide a potential means of investigation when other information sources are limited.

Channel aggradation at the Vanderhoof WSC gauge, which began in 1970 (Figure 2.5), provides further evidence of the presence and timing of a sediment wave. The presence of high flow in 1964, 1967 and 1972 makes these the most likely years for major downstream sediment movement, and the first two of these years coincide with recruitment declines. Cheslatta avulsion sediment is considerably finer than the original gravel and cobble bed material of the Nechako River, which has been essentially immobile since the onset of regulation. The period of greatest aggradation at the WSC gauge occurred between 1975 and 1995, indicating that there was a considerable lag time for the sediment wave moving down the channel. However, accumulation had already occurred downstream at site S4, suggesting that the avulsion material may have travelled in at least two waves: a more rapid, finer-textured wave that passed Vanderhoof without causing identifiable aggradation, but which deposited further downstream, and a slower, coarser wave that first appeared at the Vanderhoof WSC gauge in 1970. The three-year difference between the initiation of recruitment failure and detectable aggradation at the Vanderhoof gauge site was likely caused by sediment accumulation in the 2 km depositional reach (the spawning reach) immediately upstream of the WSC gauge site. The occurrence of such a lag is consistent with the passage of a sediment wave that would reach upstream sites first and that would move more slowly through lower gradient river sections. Alternately, the earlier indications of recruitment failure in 1964 might be due to the introduction of finer sediments first noted at site S4 between 1953 and 1966. The importance of substrate condition at spawning sites for other sturgeon (Nichols et al. 1999; McDonald et al. 2009; Du et al. 2011) provides further support for the apparent effects identified in the Nechako River.

The downstream passage of sediment load may support two competing hypotheses about causes of recruitment failure as changes have been noted for both in and off channel habitats (Rood and Neill 1987; Northwest Hydraulics 2003; Northwest Hydraulics and McAdam 2003). Rood and Neill (1987) identified a 34% loss of type I side channels (those separated by a treed island) between 1953 and 1973/74, and a 64% loss by 1986. Side channel habitats are apparently an important juvenile rearing habitat (Bennett et al. 2005), and large losses of habitats such as these would support the riparian habitat hypothesis presented by Coutant (2004). However, a number of lines of evidence suggest that in-channel changes are more likely to be the primary cause of recruitment failure.

Based on a range-wide evaluation of white sturgeon, Coutant (2004) hypothesized that recruitment failure is the result of decreased flooding of riparian habitat due to river regulation, and in particular that larval mortality is increased due to the loss of cover provided by riparian vegetation. While floodplains are critical components of fluvial systems and may therefore affect recruitment via ecosystem productivity, floodplain abstraction does not appear to have caused outright recruitment failure in the Nechako River. Prior to flow regulation, Nechako River freshets led to annual overbank flooding of river margins, but full floodplain inundation was rare (Northwest Hydraulics and McAdam 2003). Post regulation declines in flood magnitude limited the availability of off channel habitat starting in the early 1950s. Thus, the delayed recruitment failure of Nechako white sturgeon indicates that significant losses of floodplain habitat preceded the dramatic recruitment decline in 1967. Continued recruitment in the lower Fraser River (Whitlock 2007) in light of the loss of 85% of historical wetland habitat (Boyle et al. 1997) is another indication that recruitment can persist in the face of significant floodplain losses. A similar pattern is also present on the Kootenay River, where the completion of most dykes by 1940 (Constable 1957, USACE 2004) may have contributed to sporadic recruitment, but recruitment collapse did not occur until after flow regulation in 1974 (Paragamian et al. 2001, 2005). Examination of these cases clearly indicates that while loss of off-channel habitat may affect stock

productivity (Snyder and Minshall 2005), it does not appear to provide an explanation for rapid and persistent recruitment failure.

Identification of the only known spawning site in the Nechako River just upstream of the significant floodplain area at Vanderhoof (Liebe et al. 2004) (Figure 2.6) provides further evidence that recruitment failure is more likely caused by alterations to channel substrates. Losses of side channel habitats identified by Rood and Neill (1987) are spread over the 150 km of the river from Vanderhoof upstream to Cheslatta Falls, and only very limited changes were identified downstream of Vanderhoof (Northwest Hydraulics 2003). Therefore, the majority of side channel losses occurred upstream of the present spawning location. Although Rood and Neill (1987) could not precisely identify the timing of side channel losses, the identification of a sediment wave suggests they were likely lost sequentially rather than synchronously. As a result, the rapidity of the recruitment failure versus the likely progressive nature of side channel losses, in combination with the present spawning location being downstream of most lost side channels, indicates that the recruitment failure is likely not caused by the loss of side channel habitats. This comparison provides further evidence that contradicts the hypothesis that lost riparian habitat is the underlying cause of recruitment failure (Coutant 2004), and suggests that alterations in the bed substrate of main channel habitats are more likely to be causing recruitment failure in the Nechako River.

The delayed decline in recruitment relative to the completion of Kenney Dam indicates an absence of temporal correlation with the immediate effects of flow regulation and recruitment failure, as a result direct effects of flow regulation, including the decreased inundation of riparian habitats, are unlikely to be causal mechanisms of recruitment failure. Although the correlative basis of the relationship between substrate change at spawning sites and recruitment failure means the apparent relationship is not definitive, it does provide a sound basis for the hypothesis that recruitment failure is

the result of substrates changes at spawning sites. A variety of mechanisms by which increases in fine-grained sediment may limit recruitment have been proposed, including increased predation due to the loss of interstitial refuges and egg suffocation due to sand cover (Paragamian 2001; Kock 2006; NWSRI 2004). Sand movements have been observed to cover eggs in the Kootenai River (Paragamian 2001). While sand movement is apparent in the Nechako River (Northwest Hydraulics and McAdam 2003), it does not appear to be rapid enough to cause egg burial. Identification of a preference for gravel substrate by yolksac larvae but not feeding larvae (Bennett et al. 2007) suggests substrate change may preferentially affect yolksac larvae. This possibility is further evaluated in the experiments conducted in Chapters 4 and 5, which provide important validation for the hypothesized effects of substrate condition on the behaviour and survival of yolksac larvae.

Table 2.1 Relative sediment changes from air photo analysis. Symbols indicate changes (= no change, + increase, ++ large increase) between years with comparable photos. A more defined period of sediment accumulation is noted by the shaded area for site R2b. Previously published in McAdam et al. (2005). © Transactions of the American Fisheries Society, 2005, by permission.

Habitat Cluster	Habitat Unit	YEAR												
		1928	1946	1947	1951	1953	1960	1961	1966	1973	1974	1985	1990	1995
1	S1a	no detectable change												
	S1b	no detectable change												
	R1	no detectable change												
2	S2a									=				=
	S2b									+		+		
	S2b						=						=	
	R2a						=							=
	R2b						=		=	+		+		
	R2b		+								+		=	
3	S3										++		++	
	R3a					+					+			
	R3b	no detectable change												
4	S4						+				+			
	R4						+				+			

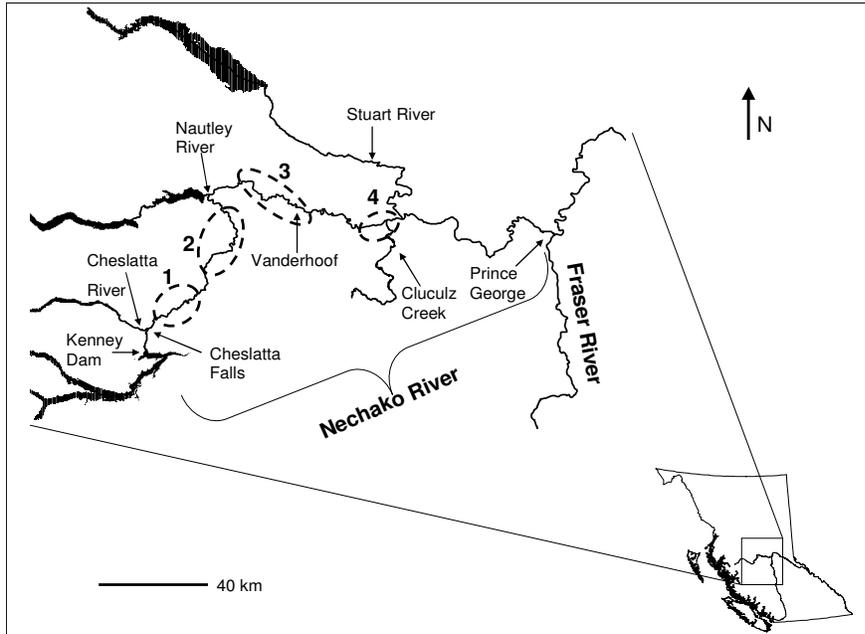


Figure 2.1 Map of the study area. Numbers indicate habitat clusters within which putative spawning and rearing habitat units are located. British Columbia is shown for reference. The spawning site is located in habitat cluster 3. Previously published in McAdam et al. (2005). © Transactions of the American Fisheries Society, 2005, by permission.

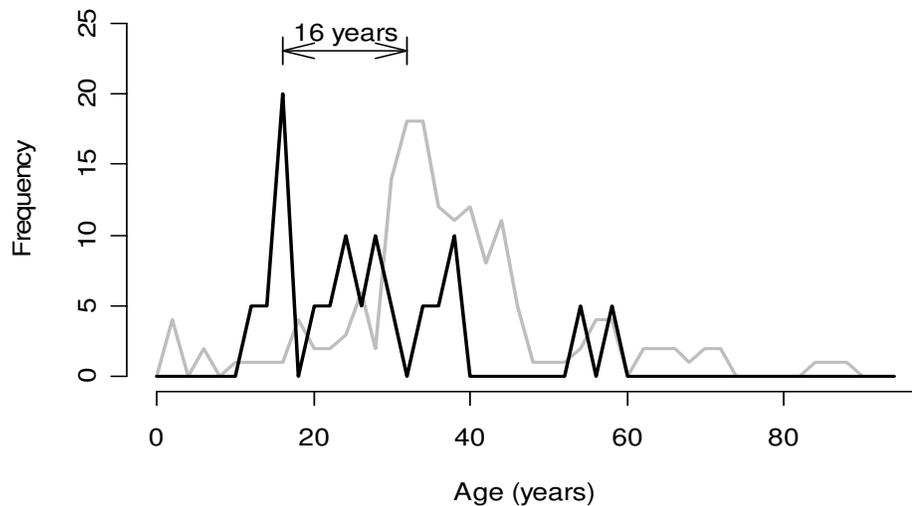


Figure 2.2 Comparison of corrected age distribution from previous studies by Dixon (1982) (black) and R, L&L (2000)(grey). Previously published in McAdam et al. (2005). © Transactions of the American Fisheries Society, 2005, adapted by permission.

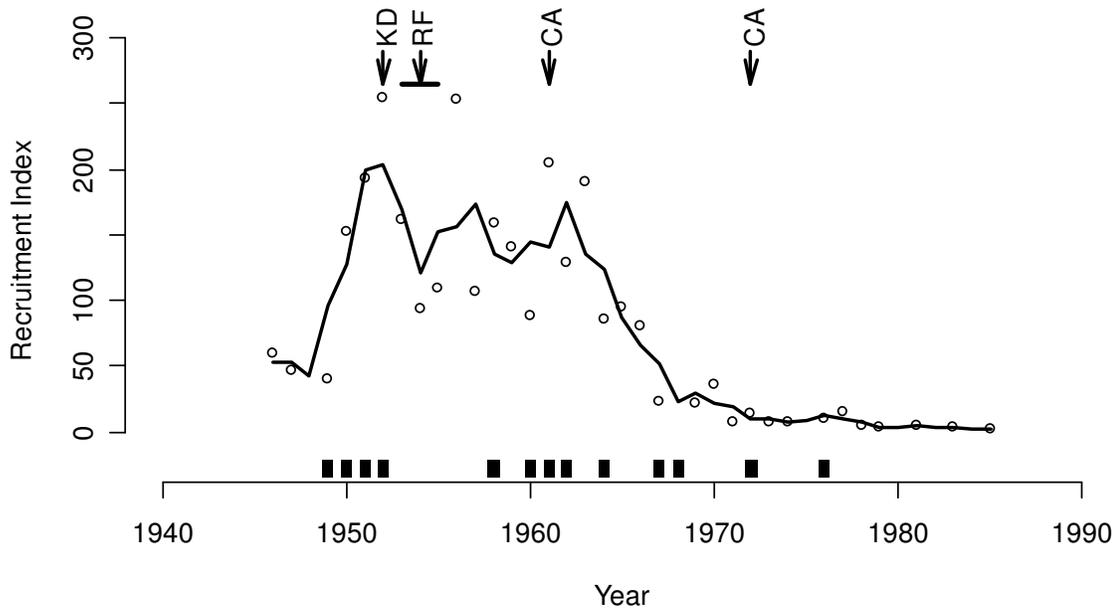


Figure 2.3 Historical pattern of projected recruitment ($M=0.08$). Blocks along x axis indicate year when flow at Vanderhoof exceeded $500 \text{ m}^3/\text{sec}$. KD = completion year of Kenney Dam, RF = reservoir fill period, CA = years of upstream sediment inputs due to the Cheslatta avulsions. Previously published in McAdam et al. (2005). © Transactions of the American Fisheries Society, 2005, adapted by permission.

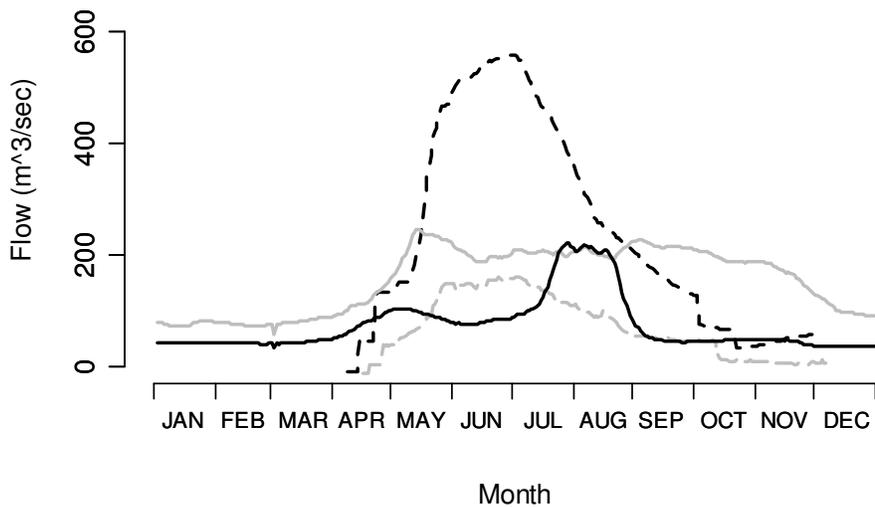


Figure 2.4 Annual hydrograph of the Nechako River above the Nautley River confluence (dashed black = mean pre-1952, dashed grey = mean 1953-56, solid grey = mean 1957-77, solid black = mean 1978-99). Flow data are unavailable from January 19-April 11 for 1950-52. Previously published in McAdam et al. (2005). © Transactions of the American Fisheries Society, 2005, adapted by permission.

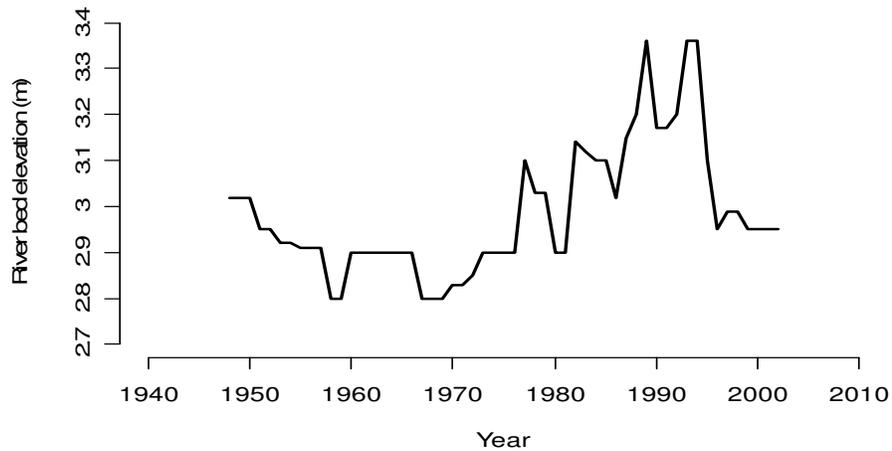


Figure 2.5 River bed elevation based on specific gauge analysis for the Water Survey of Canada gauge at Vanderhoof at a flow of 227 m³/sec. Previously published in McAdam et al. (2005). © Transactions of the American Fisheries Society, 2005, adapted by permission.



Figure 2.6 Air photo of the Nechako River at river section at site R3a on July 9, 1985 (flow= 175 m³/sec), indicating the principle spawning locations (SP) and the Water Survey of Canada gauge site (WSC). The community of Vanderhoof is located in the lower right. Previously published in McAdam et al. (2005). © Transactions of the American Fisheries Society, 2005, adapted by permission.

Chapter 3 - Recruitment history of upper Columbia white sturgeon (*Acipenser transmontanus*) and potential causes of recruitment collapse

Introduction

The identification of substrate alterations to spawning habitat as the apparent cause of white sturgeon recruitment failure in the Nechako River was assisted by the limited number of environmental changes in the watershed and the availability of suitable time series monitoring data. However, retrospective analyses typically address situations similar to the upper Columbia River (UCR; Figure 3.1), which are complicated by the variety of anthropogenic and environmental changes, limited information for some environmental variables and the presence of population substructure. Persistent catastrophic recruitment failure has now affected white sturgeon in the UCR over the last 30-40 years (UCWSRI 2002); however, the causal mechanisms of this impact are still uncertain. The presence of multiple dams, a pulp mill, a lead-zinc smelter (Table 3.1) and introduced species all represent potential large-scale and long-term impacts, and they all potentially contribute to recruitment declines. Hypothesized causal mechanisms include increased predation, changes to benthic substrates, flow regulation and contaminant effects (UCWSRI 2002; Gregory and Long 2008), but differentiating which impacts are sufficient to cause recruitment failure is a substantial challenge. Because extirpation of wild-origin white sturgeon from the UCR is certain in the absence of intervention (Wood et al. 2007), conservation risk is high. The low biological certainty regarding the causes of recruitment failure combined with the potentially substantial economic costs of restoration (e.g., due to instream habitat and flow restoration) provide strong incentives for a population-specific analysis of recruitment failure causation.

Determining causation of historical ecosystem changes is complex, and the challenge is often increased by the need to address multiple hypotheses, the complexity of large-scale ecosystems and the prevalence of anthropogenic changes (Suter 2007). Quantitative evaluations of historical

ecosystem changes are often limited by data availability as well as a lack of experimental structure and replication due to the *ad hoc* nature of retrospective studies (Beyers 1998; Fabricius and De'ath 2004; Suter 2007). All of these conditions exist with regard to white sturgeon in the upper Columbia River. In such cases, a structured evaluation of multiple hypotheses using a weight-of-evidence approach can be an effective method for evaluating potential causes of past ecological change (Suter 2007). Exploratory evaluations of correlations have also been widely employed to evaluate apparent causation of recruitment variation (see Myers et al. 1998; Planque and Buffaz 2008). However, while such quantitative approaches are appealing, they have been criticized based on the transitory nature of correlations (Walters and Collie 1994; Myers et al. 1998) and because they often evaluate proxy variables rather than hypothesized causal mechanisms (Planque and Buffaz 2008).

While retrospective evaluations will always be challenged by the previously noted limitations, perhaps the most important point with respect to all exploratory evaluations is the need for validation of proposed mechanisms by experimentation and based on comparison with other species or populations (Caughley 1994; Walters and Collie 1994). The present evaluation therefore used established weight-of-evidence methods developed in the field of epidemiology (see Fox 1991; Forbes and Callow 2002; Suter 2007) to evaluate the potential causation of white sturgeon recruitment failure. While ecoepidemiological methods have previously been adapted for natural resource applications, applications with respect to fisheries are limited (see Beyers 1998; Lowell et al. 2000; Fabricius and De'ath 2004).

Study population background

The principle area of interest in this study is the transboundary reach of the Columbia River between Hugh Keenleyside Dam and Lake Roosevelt (impounded by Grand Coulee Dam) (Figure 3.1). The small population of white sturgeon within Arrow Lakes Reservoir is also relevant to this analysis

due to its genetic similarity with fish immediately downstream of Hugh Keenleyside Dam (Nelson and McAdam 2012). Based on their genetic similarity and past movements identified by fin ray chemistry (Clarke et al. 2011), the historical spawning location of both groups was likely the same, and located upstream of Hugh Keenleyside Dam. The term upper Columbia River (UCR) white sturgeon will be used herein to refer to white sturgeon in both areas, whereas transboundary white sturgeon will refer only to fish in the transboundary reach.

Low juvenile white sturgeon abundance was identified in the early 1990s based on shifts in the size composition relative to sampling in the 1980s (Hildebrand et al. 1999; Irvine et al. 2007). The population estimate for the Canadian portion of the transboundary reach was 1,157 (95% confidence interval (CI) = 414-1900) in 2004 (Irvine et al. 2007), and 52 fish (95% CI = 37-92) were estimated to reside in Arrow Lakes Reservoir (Golder 2006d). The population estimate for the American portion of the transboundary reach was 2,037 (95% CI = 1093-3223) in 2005 (Howell and McLellan 2007), and those fish primarily reside between the upper section of Lake Roosevelt upstream from the international border.

Spawning within the UCR was first identified in the Pend d'Oreille River downstream of Waneta Dam at the confluence with the Columbia River (R. L. & L. 1994; Figure 3.1). Egg mat sampling has been conducted at that site almost annually since 1993, and spawning has been detected in all years sampled (e.g., Golder 2005a, 2010). Spawning has since been detected in Washington State at sites near Northport and China Bend (Figure 3.1), and eggs, yolksac larvae and feeding larvae have all been detected (Howell and McLellan 2007, 2009, 2011). More recently, the capture of yolksac larvae immediately downstream of Castlegar (Golder 2010) and downstream of Arrow Lakes Generating Station (ALGS) tailrace (Terraquatic Resource Management 2011) suggests the possibility of two additional contemporary spawning locations (ALGS is the power plant adjacent to Hugh Keenleyside

Dam). Egg mat sampling has also confirmed that white sturgeon residing in Arrow Lakes Reservoir spawn in the mainstem Columbia River near Revelstoke (Golder 2006d). Based on the confirmation of egg viability at multiple spawning sites, the present analysis assumes that recruitment failure results from increased mortality subsequent to fertilization. The survival of ten-month-old hatchery progeny (Golder 2006b) also indicates that mechanisms causing recruitment failure occur prior to that age.

Within the Canadian portion of the transboundary reach white sturgeon congregate in a restricted number of high-use areas within the UCR (R. L. & L. 2001). Irvine et al. (2007) identified two spatially distinct groups (or strata) within the population (strata A = Hugh Keenleyside Dam to 20 km downstream; strata B = 20km downstream to border) and estimated a consistent 3% to 5% exchange rate between them. Analysis of individual movement using telemetry and capture data also demonstrates that fish show high fidelity to one of four high-use habitat areas (Howell and McLellan 2007; Nelson and McAdam 2012). While a higher degree of movement has been suggested based on previous analysis of telemetry data (Golder 2006b), incomplete accounting for telemetry data errors (e.g., false detections, noise) suggests actual movement frequency is lower than these estimates. Geographically defined groups also show differences in growth (Van Poorten and McAdam 2010) and fin ray chemistry (Clarke et al. 2011), which provide further confirmation of restricted movement.

Identification of genetic differences between geographically defined groups using mtDNA (Nelson and McAdam 2012) but not nDNA (Schrier et al. 2011) likely reflect more rapid divergence from genetic drift of mtDNA (Zink and Barrowclough 2008) combined with the possibility of slower changes in the nuclear genome due to polyploidy. Limited divergence is also unsurprising given long generation time and the relatively short time period since the post-glacial founding of these populations (i.e. < 10,000 years or about 250 generations). While the delineation of management units for white sturgeon populations (and other species in highly-impounded rivers) is often based on dam locations, such

definitions reflect a designation that is more operational than biologically based (Reiss et al. 2009). Based on previously identified distinctions and the identification of demographic differences in this study, these groups are referred to as stocks in this analysis.

Study goals and analytical approach

The goal of this study is to undertake a retrospective analysis of white sturgeon recruitment failure in the UCR to identify potential causes, and provide guidance to experimental validation studies and future restoration. The structured weight-of-evidence evaluation was based on epidemiological methods (Forbes and Callow 2002; Suter 2007), and the selection of these methods was influenced both by the availability of historical environmental data and biological uncertainty (e.g., drift behaviour of larvae, see Chapter 4). The two prior evaluations of white sturgeon recruitment failure also utilized weight-of-evidence approaches, with Coutant's (2004) range-wide analysis and Gregory and Long's (2008) evaluation of the upper Columbia River white sturgeon based on 'listing of evidence' (see Linkov et al. 2009) and professional judgment, respectively. The principle difference in the present study is that stock structure and temporal patterns in hindcasted recruitment are specifically included in the analysis, which allows greater differentiation of hypothesized mechanisms based on population-specific data.

An additional complexity as compared to the previous chapter is the evaluation of aging inaccuracy and its effects on the estimated timing of recruitment failure. Due to potential inaccuracy (Paragamian and Beamesderfer 2003) and imprecision (Rien and Beamesderfer 1994), caution is often urged in the use of sturgeon age estimates (Rien and Beamesderfer 1994; Rossiter et al. 1995). However, despite these concerns, previous evaluations of sturgeon (e.g., Chapter 2; LeBreton et al. 1999; Paragamian et al. 2005; Woodland and Secor 2007; Smith et al. 2012) suggest that aging error may not be severe in all cases. Because population-specific age validation is not available for the UCR,

aging accuracy scenarios (no, low and high inaccuracy) were evaluated based on age validation studies of white sturgeon and lake sturgeon (*Acipenser fulvescens*) (see Brennan and Caillet 1991; Paragamian and Beamesderfer 2003; Bruch et al. 2009). In addition, comparison with the known timing of the completion of Hugh Keenleyside Dam in 1968 was used as a means to evaluate the likely degree of aging inaccuracy affecting white sturgeon in the UCR.

Similar to Chapter 2, hindcasted recruitment provides the basis for evaluations in this chapter; however, due to the prior development of clear hypotheses (e.g., Gregory and Long 2008) and the greater variety of environmental changes, a more structured process was utilized. First, I evaluated the estimated timing of recruitment failure for both stocks and an aggregated population, including potential aging error effects. I then compared stock-specific estimates of recruitment failure timing with the timing of major anthropogenic changes in the watershed (e.g., dams, pulp mill, smelter) and available environmental monitoring data. These comparisons provide important contextual information regarding the variety of anthropogenic changes present in the UCR. Such comparisons also reflect the most common type of comparison based on the known events rather than specific mechanistic hypotheses based on the species' biology. In the final component of the study I evaluated 11 recruitment failure hypotheses using a structured weight-of-evidence approach that is well established in the field of epidemiology (Forbes and Callow 2002; Suter 2007). Hypotheses were evaluated based on criteria such as the spatial and temporal similarity of expected and observed recruitment patterns, as well as experimental and stock-specific monitoring information relevant to each hypothesis. Additionally, based on the concept that factors affecting recruitment should be similar for populations occupying similar habitats (Moran 1953; Koizumi et al. 2008; Manderson 2008), hypotheses were also evaluated based on the consistency between their expected effects and observed demographic differences between stocks. The strength of this approach lies in the ability to consider multiple disparate data sources and multiple hypotheses. While proof of historical impact causation is

challenging (Fabricius and De'ath 2004; Suter 2007), the present study provides clear evidence that refutes most hypotheses and strongly supports one in particular. Because the ultimate goal of identifying the causes of recruitment failure is to reverse them, results are also discussed with regard to their implications for habitat restoration.

Methods

Source data

Data for the Canadian section of the study area were extracted from the UCR white sturgeon database on February 10, 2010 (data provided by James Crossman, BC Hydro). That database contains all capture records from past research fisheries for white sturgeon in the Canadian portion of the transboundary reach, although the present analysis only utilized data regarding individual identity (by PIT tag or Floy tag), capture location, date of capture and estimated age (based on fin rays and evaluated by at least two people). Age data for the U.S. section of the study area were provided for 124 fish by the Washington Department of Fish and Wildlife (Jason McLellan, 2315 Discovery Place, Spokane Valley, WA). Review of the Canadian database identified that about 30% of records had some irregularities (particularly with respect to capture location); these were corrected by cross reference within the database (using detailed site information that did not contain errors) and with previous versions of the database. Subsequent to quality control checks, the capture history of individuals was used to subdivide fish into geographic groups based on their area of most common capture.

The criteria for group definition were:

- HLK stock - capture locations from Hugh Keenleyside Dam to 8 km downstream.

- BRL stock - capture locations from the lower Kootenay River from Brilliant Dam, downstream to the confluence with the Columbia River (about 3.2 km), including Kootenay Eddy.
- WAN stock – capture locations from river kilometer 52-56, which includes both Fort Shephard and Waneta areas.

All fish from Lake Roosevelt upstream to the international border were assigned to a fourth group (ROOS stock). The 22 individuals with equal numbers of captures from multiple locations were excluded due to their uncertain group designation. Ties between defined areas and locations outside defined areas were assigned to the defined area of most frequent capture. Geographic groups were then sorted to identify fish with fin-ray based age estimates. To decrease potential aging error effects only the earlier estimate was included for fish with more than one age estimate.

Sufficient historical data are available only for some environmental variables, including river flow, reservoir elevation, water temperature, turbidity and some contaminants. Flow data were provided by BC Hydro or accessed from internet sources (<http://www.cbr.washington.edu/dart/dart.html>; accessed on March 10, 2010). Lake Roosevelt elevation data were provided by Bonneville Power Administration. Turbidity data were extracted from the EMS database maintained by the BC Ministry of Environment as well as from internet sources (<http://www.ecy.wa.gov/apps/watersheds/riv/station.asp?sta=61A070>, accessed May 10, 2010) for Northport Washington (Washington Department of Ecology site 61A070). Temperature (Hamblin and McAdam 2003; McAdam 2002; Tiley 2006), total gas pressure (TGP) (e.g., CRIEMP 2005) and contaminants (Kruse and Webb 2006; CRIEMP 2008) data have been summarized elsewhere and are not reproduced here.

Recruitment hindcasting

Hindcasted recruitment was calculated using the formula:

$$R_{t-a} = P_a \cdot e^{a \cdot M}$$

where P_a is the proportion of the sampled fish that were age “a” at year “t” and M is the assumed mortality rate. The assumed mortality rate of 0.04 is intermediate between the estimates of 0.108 (catch curve) and 0.027 (mark recapture), estimated by Irvine et al. (2007) for the UCR, and is similar to natural mortality estimates from the lower Fraser population (Whitlock 2007).

Three aging inaccuracy scenarios were evaluated, with the “no inaccuracy” (e.g., HLK-N) scenario based on Brennan and Caillet (1991). The “low inaccuracy” scenario (e.g., HLK-L) was based on estimated ages (EstAge) for lake sturgeon (Bruch et al. 2009) using the formula:

$$TrueAge = EstAge^{1.054796}$$

The “high inaccuracy” scenario (e.g., HLK-H) was based on analysis of Kootenay River white sturgeon and uses the following formula derived from Paragamian and Beamesderfer (2003):

$$TrueAge = \frac{\ln(1.74(\exp^{-0.0136(EstAge-4.06)}) + 0.078764)}{-0.0194}$$

Due to abundance differences between areas, particularly between Canadian and American portions of the UCR, the recruitment time series for the aggregate population was derived as the average of normalized stock-specific recruitment weighted by the population estimates for each area. Population weights were based on estimates for mature fish (corrected to 2010 using $M=0.04$), which were derived from earlier estimates in McLellan and Howell (2007) and Irvine et al. (2007). Because one population strata used by Irvine et al. (2007) encompasses both the HLK and BRL groups, the analysis used the recruitment history of those two groups combined.

I identified the number and timing of discontinuities (breakpoints) in the recruitment time series based on the identification of changes in regression coefficients using techniques described by Zeileis et

al. (2003). The likely timing of discontinuities in recruitment time series is based on evaluation of sequential F statistics (based on Chow 1960 as modified by Zeileis et al. 2002). Estimation of the number of breakpoints in the time series was based on techniques described by Bai and Perron (1998, 2003). Tests of sequential F statistics and estimation of breakpoints were conducted using the *strucchange* package (Zeileis et al. 2002) in R (Version 2.9.0, R Development Core Team 2009, <http://www.rproject.org>). For breakpoint estimation the trimming parameter was set to $h=0.15$, and significance was evaluated based on the following equation from Andrews and Plober (1994) using the *scctest* function, and p values based on Hansen (1997).

$$\exp F = \log\left(\frac{1}{\bar{i} - i + 1} \sum_{i=1}^{\bar{i}} \exp(0.5 \cdot F_i)\right)$$

Initial evaluations identified the year with the highest F statistic value for each stock and then normalized recruitment relative to the mean value for the previous three to 13 years (the historical reference period). This definition maximized the length of each reference period while excluding values immediately adjacent to likely decline years and highly variable values early in the time series. The analysis of recruitment time series utilized data beginning 20 years prior to the estimated decline year in order to limit the effects of high variability and missing data in the earlier portions of some time series. In cases where multiple break points were identified, only those representing declines leading to recruitment collapse are reported. If more than one breakpoint was associated with a recruitment decline then both are reported; in such cases the earlier breakpoint was used to identify the extent of historical data included. The absence of recent recruitment limited the identification of breakpoints near the end of the time series. In order to evaluate whether further breakpoints could be identified, four subsequent years of zero recruitment were assumed. All breakpoints identified with this modification are identified. Comparisons between groups were based on the timing of identified breakpoints and their 5% and 95% confidence intervals.

Evaluation of recruitment failure causation

A list of recruitment failure hypotheses and their inherent mechanisms (Table 3.2) was constructed by amalgamating information from the upper Columbia River White Sturgeon Recovery Plan (UCWSRI 2002), the draft species recovery strategy (DFO 2012), Gregory and Long (2008) and Hatfield et al. (2004). Evaluations of recruitment failure hypotheses were based on comparison of the HLK, WAN and ROOS stocks, as well as the aggregate population. The BRL stock was not included in the evaluation of recruitment failure hypotheses due to its small size and the resulting uncertainty in its demographic pattern (see results).

Evaluation of recruitment failure hypotheses utilized an ecoepidemiological approach based on Forbes and Callow (2002) and Suter (2007). The evaluation of temporal correlations was divided into two parts in order to identify the specific aspect of the recruitment decline being considered. Similarly, the evaluation of the biological coherence criterion was divided to identify two distinct biological questions. Scoring weights were taken from Suter (2007) and are indicated in brackets.

- 1) Temporal correlation: Is there evidence for correlation between adverse effects in white sturgeon and exposure to the causal agent in time based on:
 - a. the timing or recruitment declines? (+1/-3)
 - b. the presence of sustained recruitment failure during the collapse phase? (+1/-3)
- 2) Relative temporal difference: Is there evidence that could explain demographic differences between stocks? (+1/-3, refute)
- 3) Spatial correlation: Is there evidence for correlation between adverse effects in white sturgeon and exposure to the causal agent in space? (+1/-3, refute)
- 4) Theoretical coherence: Is there theoretical evidence of potential causation? (+2/-2)

- 5) Factual coherence: Is there evidence of causation based on findings in the upper Columbia River? (+2/-3)
- 6) Biological coherence: Is there evidence of causation between adverse impacts and recruitment failure based on:
 - a. controlled experiments? (+2/-2)
 - b. the expected life history stage affected? (+2/-2)
- 7) Removal: Has removal of the causal agent led to amelioration of effects on white sturgeon recruitment? (+2/-2)

For temporal comparisons, estimated recruitment decline timing was based on both the low and no aging error scenarios (see results and discussion regarding the high inaccuracy scenario). The consistency between hypothesized effects and observed recruitment patterns during the collapse phase was based on whether impacts were expected to show a binary, variable or positive impact pattern (see Table 3.3). For spatial comparisons, the location of the primary habitats used by each stock (Figure 3.1; Golder 2006b; Irvine et al. 2007; Nelson and McAdam 2012) was considered relative to the expected spatial impact pattern. For the evaluation of relative temporal differences, hypotheses were considered unlikely if their impact was waterborne and affected the mainstem of the transboundary reach (such impacts should affect all stocks nearly simultaneously), or if location-specific impacts occurred downstream of the primary habitat of the HLK stock.

Positive scores indicate that there is evidence supporting the question, and negative scores indicate contradictory evidence. For all coherence criteria scores of positive or negative two indicate strong evidence and scores of one indicate weak evidence. For all correlative comparisons the maximum positive score (+1) reflects the fact that correlations are not definitive indicators of causation. However, the stronger negative weighting for all correlations reflects the fact that a lack of correlation

is considered a more critical indicator (Fox 1991; Forbes and Calow 2000; Suter 2007) due to the potential to refute the hypothesis. In some cases, if the absence of either a spatial or temporal correlation was considered definitive, the hypothesis was considered to be refuted (see Suter 2007). Scores of zero were applied when no information was available. Because evaluation of scores is subjective, the scoring rationale is provided, particularly when partial scores (less than the maximum positive or negative score) were assigned.

Results

Recruitment hindcasting and aging error effects

The classification of fish into groups identified 174, 46, 163 and 124 unique and aged individuals for the HLK, BRL, WAN and ROOS stocks, respectively. The mean capture years were 1993, 1995, 1994 and 1994 for these same stocks. All stocks and the aggregate population show a similar general pattern of variation around the historical mean followed by declines to a persistent pattern of very low or no recruitment through the duration of the collapse phase (Figures 3.2 to 3.6). Significant declines were identified for all stocks ($\text{exp}F$; $p < 0.001$) except BRL ($\text{exp}F$; $p > 0.05$) (Table 3.4). For the BRL stock quantitative analysis was limited by gaps in the recruitment time series and the small number of fish in that group. With the exception of the HLK-N scenario, which shows possible declines in 1968 and 1972, only one breakpoint was identified for all stock comparisons. Two breakpoints were identified for all aging scenarios for the ALL group; however, for the ALL-N scenario these breakpoints were only evident due to extension of the recruitment time series. Breakpoints identified for the ALL group reflect its composite nature and are similar to either the declines of the HLK and ROOS stocks, or the later decline of the WAN stock and the smaller second step of the ROOS stock decline. Hypothetical aging error scenarios led to identification of earlier declines for all stocks; however, the extent of this effect differs by stock. Estimated decline timing was four, one and five years earlier assuming low

error, and 20, six and 14 years earlier assuming high error for the HLK, WAN and ROOS groups respectively. Based on differences between the mean capture year and the estimated decline year (i.e., 16 or 17 years for the WAN stock), the lower effect of aging inaccuracy for the WAN stock is apparently the result of reliance on younger fish to identify the later recruitment decline of that group.

Environmental changes for which data are available

Flow

While multiple dams affect the UCR and its watershed (Table 3.1) the most substantial changes in UCR flow occurred after completion of the Hugh Keenleyside and Mica dams (Figure 3.7), as well as the Duncan (1968) and Libby (1974) dams in the Kootenay River watershed. Winter flows have increased relative to historical conditions, with the average flow in January and February increasing from 1,100 m³/sec between 1938 and 1968 to 2,750 m³/sec for the period 1975 to 2001. Comparisons for the same years show that mean freshet flows in June and July have decreased by 48% from historical levels of 6,700 m³/sec to a contemporary average of 3,700 m³/sec. Although average contemporary freshets are diminished, high flows still occur, and freshet flows in 1997 were similar to historical average conditions (Figure 3.7).

Although the Pend d'Oreille River has 11 mainstem dams, all but 7-Mile Dam (1979) were constructed prior to 1967 (Table 3.1). The relatively low storage volume in most reservoirs on the Pend d'Oreille River means that spring snowmelt freshets are still present; however, mean June to July flows decreased by over 30% based on comparison of the years 1958 to 1964 with 1980 to 1990 (data not shown). Notable events in the Pend d'Oreille hydrograph were a distinct decrease in total outflows from Albeni Falls Dam after 1976, as well as low summer flows in 1973 and extreme low flows in 1977 (Figure 3.8).

Lake Roosevelt water elevation

Prior to 1980 Lake Roosevelt had deeper draw down and less variation in refill timing (Figure 3.9). Subsequent to 1980 drawdown was generally shallower; however, reservoir elevation still resembles early patterns in some years (Figure 3.10).

Turbidity

Contemporary turbidity data are relatively abundant, but historical data are limited. Turbidity levels at Castlegar prior to 1974 (n = 39) showed a maximum value of 10.0 NTU and averaged 2.2 NTU, whereas data after 1974 (n = 122) had a maximum of 5.9 NTU and a mean of 0.75 NTU (Figure 3.11). Plotting the pre-1974 data by date shows a small increase in average turbidity to 2.9 NTU during June and July; however, the highest historical turbidity typically occurred in February and March. Turbidity at Northport shows apparently higher values prior to 1974 (n = 25, mean = 3.6 NTU, maximum = 7 NTU) as compared to the period from 1974 onward (n = 215, mean = 1.4 NTU, maximum = 11 NTU) (Figure 3.12). Data prior to 1974 show no substantial increase in freshet turbidity (Figure 3.12), and the maximum value at Northport of 11 NTU occurred on June 4, 1997. Similarly, elevated turbidity readings were also identified for the Pend d'Oreille River (June 17, 1997 readings of 11 NTU and 13 NTU) (data not shown), but data during this period are not available for the UCR upstream of the Pend D'Oreille confluence.

Retrospective evaluation of recruitment failure hypotheses

Temporal correlation

Temporal comparisons suggest that most hypotheses were considered implausible by at least one comparison; however, data are not available for all potential comparisons (Tables 3.5, 3.6). Hypotheses also showed generally poorer temporal concordance with the timing of the WAN stock decline. The flow regulation hypothesis was considered plausible due to the similarity to in decline

timing of the HLK and ROOS stocks and the completion of Hugh Keenleyside Dam, but it was considered implausible for the WAN stock due to the later decline of that group. The similarity in recruitment decline timing and the initiation of flow regulation due to Hugh Keenleyside Dam suggests four other plausible hypotheses with temporally similar impact timing (connectivity, gas supersaturation, nutrient availability, temperature) that were also considered plausible for the HLK and ROOS stocks. However, based on similar logic these same hypotheses were considered implausible for the WAN stock due to its later decline. Because the smelter at Trail began operations over 55 years prior to recruitment failure, contaminant impacts from that source were considered unlikely. Partial scores were assigned for contaminant effects related to pulp mill effluent, as it only preceded recruitment failure by eight years. However, impacts related to the pulp mill contaminants were considered less plausible (-2) for the WAN stock due to the more extended interval until recruitment failure of that stock.

Although there is evidence of substrate alterations at all spawning sites (see Golder 2006a; Crossman and Hildebrand 2012), there is no clear temporal data. As a result, only the ROOS stock was assigned a positive score based on the effects of flow regulation on mainstem river bed substrates (Chapter 2; Reiser 1990; Petts and Gurnell 2005). Potential effects on habitat diversity were considered implausible for the Waneta group due to its later decline, and for the ROOS group because side channel habitat losses caused by the formation of Lake Roosevelt would have preceded recruitment failure by over 25 years. In contrast, for the HLK stock the formation of Arrow Lakes Reservoir would have affected floodplain habitats near the putative historical spawning site about the time of recruitment failure. While turbidity did not decrease until after recruitment failure of the HLK and ROOS stocks, partial scores were assigned due to the limited availability of historical data. Finally, changes in fish species composition were considered implausible based on the much earlier introduction of walleye in the 1960s (McMahon and Bennett 1996), particularly in comparison to the timing of the WAN stock decline.

Scoring for the aggregated population was based on the stepped decline pattern in recruitment. Because the timing of flow changes due to Hugh Keenleyside Dam (1968) and Mica Dam (1974) could conceivably lead to a stepped recruitment decline pattern, flow regulation was considered a plausible hypothesis. Similarly, for four other hypothesis which reflect impacts that would vary due to flow regulation (gas supersaturation, turbidity, nutrients and food supply, temperature) assigned scores were the same as for the HLK and ROOS groups (which were based on temporal similarity with flow regulation). Both connectivity and changes in fish species composition hypotheses were considered implausible for this group because their associated impact mechanisms are incompatible with a two-stepped decline pattern. For both categories of contaminants, scores and logic were the same as for the HLK and ROOS stocks. With regard to habitat diversity, hypothesized effects were considered implausible, but a partial score was assigned to reflect the plausibility of this hypothesis for the HLK stock.

As all stocks are undergoing recruitment collapse they were evaluated together with regard to consistency between hypothesized impacts and the sustained absence of recruitment during the collapse phase. Seven evaluations rated hypotheses as implausible and five were considered plausible based on their binary impact pattern. The most important criterion for identifying impacts as implausible was whether the hypothesized impact had a variable pattern that would only affect white sturgeon in some years. For example, TGP (CRIEMP 2005) and water temperature (McAdam 2002; Hamblin and McAdam 2003; CRIEMP 2008) were high in some years, but not all years. Similarly, both flows and turbidity were high in 1997, but because only low level recruitment was detected (see Howell and McLellan 2011) a partial negative score was assigned. With respect to waterborne contaminants, levels have decreased (CRIEMP 2008), leading to an expected positive effect on recruitment (which was not observed). A binary impact pattern associated with the initiation of the pulp mill in 1961 is dissimilar from the apparent timing of recruitment failure, but not sufficiently dissimilar to be rejected

by this criterion. In contrast, although the smelter may have led to a binary impact when it started in 1910 (Table 3.1), because recruitment failure occurred over 55 year later the more relevant patterns for this analysis are the more recent declines in contaminant levels (CRIEMP 2008). Hypothesized effects of overharvest would also have been eliminated with the closure of the sport fishery in 1996 (UCWSRI 2002), but no effects on recruitment have been detected.

Spatial correlation

Spatial comparisons generally led to considering hypotheses plausible for most comparisons (i.e., score = 1) due to the spatial proximity of impacts on either some or all stocks; however, six hypotheses were considered implausible by at least one comparison. Because both movement patterns (Nelson and McAdam 2012) and fin ray chemistry (Clarke et al. 2011) suggest that the HLK stock is the only group of fish that shows spatial overlap with the connectivity limitations due to Hugh Keenleyside Dam, this hypothesis was considered to be refuted based on a lack of spatial correlation for the WAN and ROOS stocks. For the HLK stock, contemporary and historical use of habitats from Castlegar upstream would lead to little or no spatial overlap with smelter-derived contaminants. Based on the assumption of historical spawning by the HLK stock upstream of Hugh Keenleyside Dam and the presence of recruitment failure for fish still residing in Arrow Lakes Reservoir, gas supersaturation and changes to fish species composition were also considered implausible because such impacts have not been identified in those areas. Based on a similar rationale, contaminant impacts related to the pulp mill at Castlegar were given a partial score due to the potential for some historical spatial overlap. For the WAN group, changes to habitat diversity were considered implausible because this group in particular occupies an exclusively riverine section of the Columbia River.

Relative differences of the WAN stock

Due to the identification of later recruitment failure for the WAN stock, hypotheses were evaluated based on their ability to explain the lagged response of this group (the relative difference criterion). Because all white sturgeon in the transboundary reach reside in the mainstem river from the stage of feeding larvae onward, all should be similarly exposed to waterborne impacts (unless impacts originate in tributaries). Waterborne effects to the mainstem UCR therefore should not lead to the observed relative differences in the WAN stock. As a result, eight hypotheses that rely on a waterborne mechanism were considered implausible. Spatial comparisons also suggest that six hypotheses are inconsistent with the pattern of a later impact for the WAN stock that resides between two stocks that show earlier declines. For example, effects due to altered species composition and increased predator abundance are considered unlikely because they provide no mechanism by which upstream and downstream stocks would be affected synchronously, but prior to the WAN stock. Similar to the evaluation of spatial correlation (above), the location of the lead-zinc smelter at Trail should not lead to an earlier effect on the HLK stock, which generally resides upstream of that location (Figure 3.1; Nelson and McAdam 2012; Clarke et al. 2011). The hypothesis regarding geomorphological change was the only hypothesis considered plausible based on the evaluation of the relative difference between stocks.

Coherence criteria

Evaluations based on theoretical coherence show no differentiation between hypotheses except overfishing (Table 3.5), which was considered implausible based on both the expected population at the time of recruitment failure (UCWSRI 2002) and theoretical evaluations of low population effects for white sturgeon (Jager et al. 2010) and lake sturgeon (Schueller and Hayes 2011). The life stage criterion also led to fairly straightforward results, and suggest that overharvest and connectivity are implausible because neither impact is expected to affect early life history or early juvenile phases.

With respect to the factual coherence criterion, suitable data were unavailable for four hypotheses (Table 3.5), but scores were evaluated for seven criteria. For example, with respect to flow regulation, other than temporal correlations (which are scored separately) there are no monitoring data (e.g., sturgeon movement) for the upper Columbia River that specifically indicate a biological effect for a particular flow regime. The same is true for gas supersaturation and turbidity. The score for the overharvest hypothesis reflects the presence of a sport harvest until 1996. The low plausibility scoring for contaminants was based on Kruse and Webb (2006), who found no clear indication of contaminant effects based on tissue analysis and ambient contaminant levels, and Vardy et al. (2011), who found that ambient water quality guidelines provide sufficient protection from waterborne copper, cadmium and zinc. However, a partial score was assigned because contaminant levels were apparently higher historically (CRIEMP 2008) and because recent laboratory studies identified impacts to benthic invertebrate survival (Fairchild et al. 2012). Geomorphological change was considered plausible based on the presence of embedded substrates at the Waneta, Northport and Revelstoke spawning sites (Golder 2006a; Tiley 2006; Jason McLellan, Colville Confederated Tribes, pers. comm.) and based on the drift patterns of yolk sac larvae (see discussion).

Partial scores for hypotheses regarding changes to food supply, thermal regimes and fish species composition acknowledge that impacts have been observed, but are not considered severe. For example, elevated temperatures are likely responsible for some egg mortality (Golder 2005, 2006a, 2010), but sufficiently high temperatures do not occur in all years. Additionally, while growth limitations have been identified for the WAN stock (Van Poorten and McAdam 2010), other stocks show high growth rates (Golder 2007). With regard to altered fish composition, walleye have been observed to prey upon juvenile white sturgeon (UCWSRI 2002), but gut content analysis of walleye does not indicate a strong predation effect (Howell and McLellan 2007, 2009). Changes in habitat diversity were rated implausible because the transboundary reach flows within a steep-sided intermountain river

valley, and off channel habitat was very limited even prior to flow regulation (Northwest Hydraulics 2007).

Evaluation based on the biological coherence criterion was limited because laboratory studies have examined potential impact mechanisms for only six hypotheses. Positive rankings related to geomorphological change, gas supersaturation, turbidity and temperature were based on the identification of increased mortality in the absence of interstitial habitat (Chapter 4, 5), elevated larval mortality due to gas supersaturation (Counihan et al. 1998), decreased larval predation at higher turbidity (Gadomski and Parsley 2005a) and decreased early life history survival at elevated temperatures (Wang et al. 1985), respectively. A negative score was assigned with respect to heavy metal contaminants based on Vardy et al. (2011), who found that current water quality guidelines provide sufficient protection from the waterborne copper, cadmium and zinc. However, a partial negative score was assigned due to the limited number of metals examined, and due to potential contaminant effects on benthic invertebrates (Fairchild et al. 2012). The partial positive score for the potential effects of altered fish community was based on the identification of relatively low predation by walleye on white sturgeon larvae (Gadomski and Parsley 2005b).

Four of eleven hypotheses received a zero score for the removal criteria because there is no indication that their associated impacts were removed or diminished at any time after they began. Over-harvest received a score of -2 because harvest impacts should have ceased with the fishery closure in 1996, but no recruitment effect has been observed. Both contaminants and gas supersaturation received low scores because the severity of both has declined (see Aspen Applied Sciences 1998; CRIEMP 2005, 2008) with no attendant recruitment effect. Temperature received a score of -2 because temperatures near the limits identified by Wang et al. (1985) do not affect all spawning sites and are not present in all years. Scores for flow and turbidity hypotheses were assigned

partial positive scores due to the fact that both high flow and elevated turbidity could have contributed to the low level recruitment seen in 1997 (Howell and McLellan 2011). However, partial scores were assigned because recruitment was only partially restored, and the fact that flow could affect recruitment through a variety of indirect mechanisms means that causal links with these two hypotheses are not definitive. The positive score for the geomorphological change hypothesis was based on the identified benefits of substrate restoration at the Revelstoke spawning site (Crossman and Hildebrand 2012) at in the Nechako River (Chapter 5).

Discussion

Due to their longevity, sturgeon provide a rather unique opportunity for the investigation of long-term recruitment patterns and the effects of habitat alteration. The identification of demographic differences between white sturgeon stocks in the UCR confirms previous identification of spatial habitat fidelity (Van Poorten and McAdam 2010; Nelson and McAdam 2012), and the maintenance of such differences over 30 years after recruitment declined demonstrates the long-term temporal stability in habitat use. Compared to the two prior evaluations of white sturgeon recruitment failure (Coutant 2004; Gregory and Long 2008), the consideration of temporal patterns and stock structure were important advancements that allowed greater differentiation between hypotheses. Utilization of an epidemiological approach also provided a structured weight-of-evidence evaluation of ecological changes, as well as a transparency that is often required for resource management decisions (Forbes and Callow 2002; Suter 2007).

The identification of substrate change at spawning sites as the probable cause of recruitment failure was based on multiple lines of evidence, and is therefore considered robust. While irrefutable proof of this proposed mechanism may ultimately require the reversal of recruitment declines, my findings are consistent with effects identified for other white sturgeon populations (Chapter 2;

Paragamian et al. 2009) and other sturgeon species (Nichols et al. 2002; Du et al. 2009). In combination with the experimental laboratory (Chapter 4) and field studies (Chapter 5; Kerr et al. 2010; Crossman and Hildebrand 2012), the present results should increase certainty regarding historical causes of recruitment decline and help shift the focus of conservation efforts toward habitat restoration.

Recruitment decline patterns and potential aging error

Although long-term evaluations of year class strength may be subject to spurious correlations due to aging inaccuracy and autocorrelation (Bradford 1991; Rien and Beamesderfer 1994), drastic recruitment failures are still readily apparent in recruitment time series (see Chapter 2; Ireland et al. 2005). Hindcasted recruitment showed consistent patterns for all stocks (except BRL), with the recruitment index historically varying around a relatively stable running mean followed by declines to sustained low (near zero) recruitment. While aging imprecision will smooth apparent decline patterns (discussed below), evaluations based on white sturgeon younger than age 25 should be minimally affected by inaccuracy due to the more limited age estimation errors for younger age classes (present results; Rien and Beamesderfer 1994; Bruch et al. 2009). The present analysis also meets the four principle assumptions related to the use of recruitment residuals (see Catalano et al. 2009) because 1) catchability is similar for fish over 90 cm (Elliot and Beamesderfer 1990); 2) adult mortality rate has not changed dramatically due to impoundment, based on the similarity of natural mortality rates (Irvine et al. 2007) with estimates from unimpounded populations (Whitlock 2007); 3) recruitment varies around an apparently stable mean both before and after recruitment failure; and 4) the large number of year classes means mortality rates of fish vulnerable to sampling should be similar both before and after recruitment failure.

The distinct timing of recruitment failure for the WAN stock in all inaccuracy scenarios, coupled with limited overlap with the confidence intervals for the HLK and ROOS stocks, provides clear evidence

that the WAN stock is demographically distinct. The mechanisms by which such a spatially-restricted group is maintained are biologically interesting because homogeneity over larger spatial scales is commonly suggested for this species (Setter and Brannon 1992; Drauch-Schrier et al. 2011). However, with regard to the present study objectives, demographic differences indicate that the onset of recruitment failure is somehow different for this stock. While the stepped decline pattern of the ROOS stock suggests demographic links between the WAN and ROOS, such links are likely due to downstream drift by early life stages (see Chapters 4 and 5), and probably do not affect the distinction of the WAN stock. Notably, a similar relationship is not apparent with the HLK stock, which may limit potential rescue effects between these two stocks.

Although age validation is a fundamental requirement for the evaluation of population dynamics (Beamish and McFarlane 1983), full age validation is unavailable for many species (Campana 2001). Evaluation of aging accuracy therefore addresses an important area of uncertainty in the analysis of sturgeon population dynamics as caution is regularly suggested when using fin-ray based age estimates (e.g., Rien and Beamesderfer 1994). As the interval between the timing of recruitment failure and the mean capture year ranged between 17 and 23 years in the present analysis, estimates of recruitment decline timing were primarily based on relatively young fish. This range limited the effects of inaccurate aging and explains why outcomes for the no and low inaccuracy scenarios showed relatively minor differences (e.g., a one year difference for the WAN group). While aging error cannot be ignored, for fish over 25 years (present study) errors in age estimation accuracy appear to represent a tractable uncertainty. The relative accuracy of the no and low accuracy scenarios is also suggested by the apparent recruitment effects associated with Keenleyside Dam on the HLK stock (see HLK specific analysis) and the fact that the year that dam was completed (1968) lies within the confidence intervals for both the HLK-N and HLK-L scenarios.

In contrast to the good agreement between the low and no inaccuracy scenarios and the completion timing of Hugh Keenleyside Dam, the correction factor based on Paragamian and Beamesderfer (2003) (the high inaccuracy scenario) led to much earlier estimates of recruitment failure. In particular, the HLK-H scenario estimated that the HLK stock would have declined in 1951, prior to major anthropogenic changes to the primary areas this stock was assumed to occupy (i.e., the UCR from Castlegar upstream). While a variety of changes in tributary watersheds might be compatible with the WAN-H and ROOS-H scenarios, based on the estimated timing for the HLK-H scenario the high inaccuracy indicated by Paragamian and Beamesderfer (2003) apparently overestimates aging inaccuracy for white sturgeon in the UCR. Golder (2005b) also suggested that the analytical methodology may contribute to the bias identified by Paragamian and Beamesderfer (2003). Because it appears to overestimate effects, the high inaccuracy scenario was not included in the evaluation of the causes of recruitment failure. Paragamian and Beamesderfer (2003) acknowledged potential overestimation if growth changed over time, but suggested that a stable Fulton's condition factor was evidence of stable growth. However, that indicator may be insufficient based on the identification of increased condition factor with length for lake sturgeon (Beamish et al. 1996).

While the timing of recruitment failure was the primary indicator used to evaluate causation, the rate of recruitment decline also provides insights, though it is less definitive. Unfortunately, recruitment decline rates cannot be evaluated with certainty due to the smoothing effects of imprecision. For example, based on mean capture ages between 17 and 23 years, and assuming imprecision based on Rien and Beamesderfer (1994), a rapid recruitment failure within one year could be smoothed to appear as a seven to nine year decline. Despite that potential limitation, all stocks show relatively abrupt recruitment declines, or in the case of the ROOS stock distinct stepped changes, which suggests that recruitment declines may indeed have been fairly rapid. Observation of recruitment time series suggests that declines occurred over about three to five years for the HLK and

WAN stocks and in the Nechako River (Chapter 2); smoothing effects in those cases may therefore be less than predicted based on Rien and Beamesderfer (1994). The possibility that recruitment declined rapidly implies that impacts associated with longer-duration changes, such as changes to the fish community, might be less likely causes of recruitment failure. However, even given the consistent observation of rapid recruitment declines, uncertainty regarding the true decline rate limits the utility of this criterion in the evaluation of recruitment failure hypotheses.

Evaluation of recruitment failure causation

Comparing the timing of recruitment failure with the timing of major anthropogenic habitat changes in the UCR is the simplest approach to evaluating causes of recruitment failure, but provides limited resolution of potential causation. The construction of Grand Coulee Dam and most dams on the lower Kootenay River and Pend d'Oreille River preceded recruitment declines by many years (over 30 years in the case of Grand Coulee Dam), which suggests that impacts caused by the creation of Lake Roosevelt and loss of tributary access were not a primary cause of recruitment failure. By comparison, the recruitment declines for the HLK and ROOS stocks did occur at about the same time as the initiation of substantial upstream regulation of mainstem Columbia River flow in 1968. The completion of the Duncan, Hugh Keenleyside, Libby and Mica dams, all within a six-year period from 1968 to 1974, led to a 48% decrease in the average contemporary freshet volume, as well as multiple associated environmental changes (see Hamblin and McAdam 2003; Pieters et al. 2003; Matzinger et al. 2007). However, the temporal similarity between the initiation of flow regulation and recruitment declines for the HLK and ROOS stocks does not identify a specific causal mechanism, nor does it explain the decline timing of the WAN group.

The absence of any clear identification of potential recruitment failure causation based on comparison with major projects and some of their associated environmental changes (discussed below)

reflects the general challenge of retrospective evaluation of ecological changes (see Beyers 1998; Fabricius and De'ath 2004; Suter 2007). Because river flow is a fundamental driver of the structure and productivity of riverine ecosystems (Petts 1985; Bunn and Arthington 2002; Moyle and Mount 2007) it is not at all surprising that flow changes are associated with recruitment failure. However, more quantitative evaluation of such correlations would still provide little or no proof of underlying mechanisms. Under such circumstances, the weight-of-evidence evaluation of multiple hypotheses that specifically address potential impact mechanisms provided the best approach for the evaluation of putative causal mechanisms.

Compared to the two prior studies of white sturgeon recruitment failure (Coutant 2004; Gregory and Long 2008), which were based on a listing of evidence approach (see Linkov et al. 2009) and best professional judgement, respectively, the key innovation in the present study was consideration of temporal recruitment patterns and stock structure. Both spatial and temporal patterns provided critical contrast for hypothesis evaluation. Comparisons based on the relative differences in recruitment decline timing (i.e., the later decline of the WAN stock) provided the most definitive evaluations because most hypotheses were incompatible with the observed difference in recruitment failure timing of the WAN stock. Even excluding that criteria, geomorphological change was still identified as the most plausible mechanism, which indicates that both the conclusions and analytical approach are robust. While selected scores for individual comparisons are subjective (for example, the differentiation between a score of -2 and -3), the consideration of multiple criteria in the overall assessment suggests that conclusions should not be affected by small variation in individual criteria scores. Furthermore, the agreement with both field- and laboratory-based findings for other white sturgeon (Chapter 2, 4, 5; Paragamian et al. 2009) and other sturgeon species (see Kerr et al. 2010; Dumont et al. 2011), provides further support both for the evaluation methods and outcomes.

Although correlations cannot prove causation, their utility in the present investigation is their ability to disprove hypotheses based on a lack of temporal or spatial correlation (Suter 2007). For example, the later decline of the WAN stock provides very clear distinctions between hypotheses because the mechanisms implied by most hypotheses are incompatible with the presence of time lags between adjacent stocks. Because demographic differences often reflect differences in environmental factors affecting recruitment (Moran 1953; Manderson 2008), demographic differences between stocks were assumed to reflect differences in habitat use. As a result, recruitment failure hypotheses that rely on a waterborne mechanism (e.g., turbidity, flow regulation, waterborne contaminants) provide no reasonable explanation for the later decline of the WAN stock because all fish occupy the same river from the stage of feeding larvae onward. Similar to the use of demographic asynchrony to identify stocks for other species (Myers et al. 1997; Fox et al. 2000; Koizumi et al. 2008), the demographic distinctness of the WAN stock provides critical diagnostic information, and only two hypotheses (overharvest and geomorphological change) appear compatible with such a pattern (and overharvest is considered unlikely by other criteria). Two important advantages of this approach were 1) that aging error effects should be eliminated (because all groups are assumed to be affected by the same degree of aging error) and 2) limited effects due to limited environmental data availability (because expected patterns are derived from hypotheses). The identification of geomorphological change as the best supported hypothesis by methods that should not be sensitive to aging inaccuracy effects (i.e., relative differences) and by those that should be (other temporal criteria) further indicates that errors due to aging inaccuracy were sufficiently addressed within retrospective analyses.

Although evaluation based on the relative differences in recruitment failure timing may be sufficient to identify substrate changes as the probable cause, the divergent views regarding recruitment failure causation based on professional judgment (Gregory and Long 2008; only one of five hypotheses was considered implausible) support the need for more detailed consideration of all

hypotheses. Based on their description in the recovery plan for the UCR (UCWSRI 2002), three hypotheses (overharvest, habitat diversity, connectivity) represent general concerns regarding either sturgeon or river regulation impacts, but appear to have limited supporting evidence with regard to white sturgeon in the UCR. For example, hypothesized effects on habitat diversity reflect concerns regarding losses of off-channel and floodplain habitat, which are generally considered important attributes of sturgeon habitat (Bemis and Kynard 2002; Coutant 2004). However, such habitats were historically limited in the transboundary reach. Although floodplain habitat was inundated due to the creation of Lake Roosevelt (UCWSRI 2002), that habitat (Marcus Flats) was affected well before recruitment failure occurred. Decreased inundation of riparian habitat was hypothesized to provide a general explanation for recruitment failure (Coutant 2004), but the present evaluation suggests that effects to riparian channel habitat provide a poor explanation for recruitment failure of white sturgeon in the UCR (see also Chapter 2). This is particularly true for the WAN stock, which principally resides in areas of the transboundary reach that never contained substantial riparian habitat.

Overharvest and connectivity effects also appear implausible based on fairly straightforward comparisons. Due to their longevity and late maturation, white sturgeon are particularly prone to overharvest (Boreman 1997), and severe population declines have been identified for multiple sturgeon species (Birstein 1993; Pikitch et al. 2005; Ruban 2005). However, the fact that harvest affects juveniles and adults suggests harvest might only exert an effect via Allee effects. Even at current population levels impacts are considered unlikely on a theoretical basis (Jager et al. 2010; Schueller and Hayes 2011). Furthermore, continued recruitment in the upper Fraser River, which contains only about 125 adult white sturgeon (Yarmish and Toth 2002), suggests very small populations can sustain themselves. With regard to connectivity, while Jager et al. (2001) suggest that larval mortality may result from entrainment and lost connectivity due to dams, such effects are considered unlikely in the present case. First, because downstream movements out of Arrow Lakes Reservoir by juveniles and adults (based on

fin ray chemistry; Clarke et al. 2011) suggest early life history stages are not affected. Additionally, at the downstream end of the transboundary reach, the large distances upstream of Grand Coulee Reservoir and the much earlier formation of Lake Roosevelt both suggest that larval losses due to the presence of the reservoir are unlikely.

The presence of sustained recruitment failure throughout the collapse phase also provides a valuable diagnostic criterion, and only some hypotheses are compatible with such a pattern. For example, both temperature and TGP are elevated due to river regulation (Hamblin and McAdam 2003; R. L. & L. 1995; CRIEMP 2005) and both may decrease early life history survival (Wang et al. 1985; Counihan et al. 1998; Boucher 2012). However, elevated levels do not occur in all years (see Hamblin and McAdam 2003; CRIEMP 2005), nor do they occur at all spawning sites (see Golder 2005a, 2010; Howell and McLellan 2007, 2009; Terraquatic Resource Management 2011). Additionally, with regard to the impacts of gas supersaturation, while Counihan et al. (1998) identified that elevated TGP has a strong effect on larval survival, the fact that all white sturgeon life stages typically reside below the compensation depth suggests that larvae would rarely be affected by such impacts.⁵ Additionally, TGP levels have been substantially reduced due to upgrades at all three hydroelectric plants feeding into the transboundary reach, but without any attendant recruitment effect.

The possibility that turbidity decreases may have caused recruitment declines is of particular interest due to the proposal to experimentally increase turbidity as a means to restore recruitment (BC Hydro 2005). The possibility of effects due to decreased turbidity is supported by local knowledge indicating elevated historical turbidity (UCWSRI 2002; Gregory and Long 2008) and the general tendency of dams and impoundments to decrease downstream turbidity (Petts 1985). Demonstrable effects on predation upon larvae and juvenile fish (Johnson and Hines 1999), including white sturgeon

⁵ Susceptibility to dissolved gas supersaturation decreases with depth because increased pressure prevents gases from coming out of solution to form bubbles.

(Gadomski and Parsley 2005a), also support this hypothesis, and a similar hypothesis has been suggested to explain recruitment declines of pallid sturgeon (Dryer and Sandoval 1993). However, even though historical data are limited, they contradict the assessments based on local knowledge and indicate no concordance with the observed patterns of recruitment failure. Historically, turbidity at Castlegar was relatively low, which was probably due to the settlement of fine particulates within the historical Arrow Lakes (depth > 200m; see Northwest Hydraulics 2007; Matzinger et al. 2007). Additionally, historical data show that the highest historical values occurred outside the spring freshet (i.e., not during the spawning period), and the relatively small decrease in turbidity occurred after the initiation of recruitment failure. Combined with the fact that historical turbidity was substantially lower than the 40-60 NTU at which larval predation declined in laboratory experiments (Gadomski and Parsley 2005a), turbidity changes provide an unlikely explanation of recruitment failure for UCR white sturgeon based on both their magnitude and timing. Although recent low level recruitment in 1997 coincides with the presence of elevated turbidity in that year (Figure 3.11; Howell and McLellan 2011), high flows in 1997 would also have been correlated with a variety of environmental changes. Therefore the suggestion that elevated turbidity plays a causal role cannot be substantiated.

Although regulation of the UCR flow has led to fundamental biotic and abiotic changes to the riverine ecosystem, hypotheses regarding hydrograph alterations and turbidity were both categorized as variable impacts because both factors occasionally reach historical levels. While low-level wild recruitment occurred in 1997 (Howell and McLellan 2011) when both flow and turbidity reached historical levels during the spawning period (Figures 3.7, 3.11), evaluation of length class abundance shows that abundance of the 1997 cohort was relatively low. As a result, this effect was not considered to represent restoration of historical recruitment. Additionally, due to the correlation of multiple potential effects with high flows (e.g., substrate movement), even the presence of a detectable recruitment pulse provides limited information regarding apparent causation. Similarly, white sturgeon

recruitment was not fully restored in response to 'natural' or anthropogenic flow experiments in the Nechako and Kootenai rivers (Chapter 2; McDonald et al. 2010), which suggests that flow alone does not provide a sufficient explanation for recruitment declines.

The previous investigation of recruitment failure by Gregory and Long (2008) suggested contaminant impacts were unlikely based on professional judgment; however, the presence of significant historical contaminant inputs (e.g., 400 MT of slag daily from prior to 1930 until 1995; Northwest Hydraulics 2008), international interest in potential contaminant effects (Du Bey and Sanscrainte 2004) and recent laboratory investigations (Vardy et al. 2011; Fairchild et al. 2012) all suggest that further attention to contaminants is valuable. The two major contributors of contaminant loading to the UCR were Celgar's pulp mill and Cominco's lead-zinc smelter, and both facilities led to substantial historical contaminant inputs (CRIEMP 2008). However, upgrades at both facilities (Celgar - 1993; Cominco - 1980 to 1997) led to water quality improvements (CRIEMP 2008). Declines in ambient levels of all waterborne contaminants (including multiple metals, PCBs, dioxins, furans) related to pulp mill and smelter inputs (except polybrominated diphenyl ethers; CRIEMP 2008) without any positive change in recruitment provides further support for the suggestion that these are unlikely causes of recruitment failure. While a variety of contaminants are present in white sturgeon tissues there is no indication that contaminant loadings are at potentially lethal levels (Kruse and Webb 2006). With respect to copper, cadmium and zinc, toxicological studies indicate that white sturgeon embryos, larvae and early juveniles would be protected by current water quality regulations (Vardy et al. 2011). Contaminant-based explanations therefore appear unlikely for a variety of reasons. First, waterborne contaminants cannot explain the later decline timing of the WAN stock. Additionally, the recruitment failure of the HLK stock, which primarily utilizes habitats upstream of inputs from the lead-zinc smelter, and recruitment failure of other populations (Chapter 2, Paragamian et al. 2009) suggest that recruitment failure can be explained without contaminant effects. Finally, the long time period

(particularly for smelter-related contaminants) over which both elevated contaminant levels and recruitment were present suggests contaminant effects are unlikely to have been the primary cause of recruitment failure.

One notable exception to the general improvements in water quality within the UCR is that substrate quality indicators are still exceeded for multiple metals at Waneta (CRIEMP 2002). While some toxicological tests showed effects on benthic invertebrate growth, but not on survival (CRIEMP 2008), recent studies identify strong survival effects upon benthic invertebrates (Fairchild et al. 2012). Combined with hypothesized habitat changes due to geomorphological changes, alterations to the spatial location of slag deposition could affect contaminant exposure levels for some life stages. Such an effect might lead to impacts upon the ROOS stock in particular as the location of slag deposition at the inlets to Lake Roosevelt conceivably changed in response to upstream flow regulation. However, such a mechanism would have no effects on the ALGS or Revelstoke spawning sites. Additionally, any mechanisms that include the ingestion of contaminants (i.e., while feeding) contrast with the previous suggestion (present study; Chapter 2) that habitat impacts at spawning sites would primarily affect the embryo and yolk sac larvae stages (i.e., pre-feeding larvae). While this contrast does not rule out the possibility of contaminant effects, it does suggest that they may provide only a partial explanation for recruitment failure.

Although nutrient changes were identified as implausible based on an inability to explain the unique timing of the WAN stock, differences in food availability do affect adult growth in that stock (Van Poorten and McAdam 2010). The identification of nutrients and food supply limitations as potential contributors to recruitment failure is also suggested by the presence of nutrient-trapping by upstream reservoirs (Pieters et al. 2003) and the possibility of larval mortality due to food limitations (Howell and McLellan 2011). However, more detailed evaluation of this hypothesis suggests support

may be limited. The effects of impoundment on downstream nutrient regimes can be complex. For example, both the conversion of large lakes to reservoirs (Matzinger 2007) and reservoir inundation (Stockner et al. 2000) would have initially increased downstream nutrient levels. As a result, the expectation of a delayed decrease in downstream nutrient levels relative to the construction of both the Hugh Keenleyside and Mica dams suggests that nutrient decreases occurred after recruitment failure. In addition, a fertilization program is currently in place to address the oligotrophic condition of Arrow Lakes Reservoir, and the absence of a recruitment response also suggests that upstream nutrient conditions are unlikely to have contributed to recruitment failure.

Apparent mechanism of geomorphological effects

Geomorphological change is the only hypothesis that is not considered unlikely by any criteria. While data specific to the temporal pattern of effects in the UCR are relatively limited, this hypothesis shows consistent plausibility based on all coherence criteria. Additionally, the comparison based on the relative differences in recruitment pattern provides definitive support for this hypothesis. The tributary spawning location makes the WAN stock unique relative to the other two stocks, and the fact that flow and substrate are primarily influenced by tributary conditions may explain the delayed onset of recruitment failure for this stock.

Similar to all other sites, the proposed mechanism of recruitment failure for the WAN stock is the loss of interstitial habitat within substrates at spawning sites; however, the principle difference at that location is that spawning occurs within the Pend d'Oreille plume. Based on a variety of evidence I propose the following explanation for the mechanism and timing of recruitment failure related to the Waneta spawning site. Due to the upstream proximity of Waneta Dam, suspended sediment inputs would be minimal from the Pend d'Oreille River. Additionally, the location of the Pend d'Oreille plume along the southeast bank of the UCR (Figure 3.13) should limit the incursion of mainstem-derived

sediment into the spawning area under most conditions (i.e., suspended sediments and bedload should not move perpendicular to the prevailing current). The exception to the protective effects of tributary flow is that flow regulation can lead to near zero flow in the Pend d'Oreille River, and under such conditions the mainstem Columbia River is the primary hydraulic influence on the Waneta spawning area (Figure 3.13; Fissel and Jiang 2007). During periods of low flow in the Pend d'Oreille River, fine substrates originating from the Columbia River mainstem therefore could affect conditions at the Waneta spawning site.

The presence of metallurgical slag at the Waneta spawning site (Golder 2006a), which originated from smelter located upstream on the mainstem Columbia River, indicates that mainstem bedload has indeed moved into the spawning area. While the exact timing of such movements has not been determined, extended periods of extreme low flow in 1977 (Figure 3.8) presumably allowed sustained movement of mainstem-origin fine substrates into the spawning area. Such an effect is consistent with the modelled hydraulic effects on the confluence area (Fissel and Jiang 2007), the timing of extreme low flows in the Pend d'Oreille River and the timing of the WAN stock recruitment failure.

Photographic evidence and visual observation (Golder 2006a) indicate that substrates at the Waneta spawning area consist primarily of embedded cobble, which is indicative of degraded conditions at other spawning locations (Chapter 2; Triton 2009; Crossman and Hildebrand 2012). Similar to the Nechako River (Triton 2009), the dominance of yolksac larvae in drift samples downstream of the Waneta spawning site (Golder 2006a) also indicate a degraded substrate condition that provides limited hiding habitat. Given that embedded substrates decrease egg survival (Forsythe 2010) as well as yolksac larvae hiding, survival, growth and development (Chapter 4; Boucher 2012; Crossman and Hildebrand 2012), drift by yolksac larvae provides additional evidence of degraded substrate conditions at the Waneta spawning site. Biological validation of this proposed mechanism is

also pursued in Chapters 4 and 5; however, further hydraulic modelling could provide a detailed understanding of the recruitment failure mechanism at this spawning site.

Given that the spawning location for the ROOS group is only about 30 km downstream from the Waneta spawning site, similar impacts would be expected to affect both sites. With regard to substrate conditions at the Northport spawning site, the high proportion of sand in that reach of the Columbia River (Besser et al. 2008) and the semi-embedded large cobble at the Northport spawning area specifically (Jason McLellan, Colville Confederated Tribes, pers. comm.) are both indicative of degraded spawning substrate (Chapter 2, 4). Additionally, similar to both the Nechako River (Triton 2009) and the Waneta spawning site (e.g., Golder 2006a, 2010), the prevalence of yolksac larvae in drift samples from some years (e.g., 2005 – 75% of larval captures were yolksac larvae; Howell and McLellan 2007), suggests the presence of degraded substrate conditions (Chapter 4). However, the predominance of feeding larvae in drift captures for other years (e.g., 76% and 73% in 2006 and 2007; Howell and McLellan 2009, 2011) suggests substrate conditions are less degraded than other sites in the UCR.

The regular detection of feeding larvae at this site without detection of later life stages suggests that decreased survival at the initiation of feeding also contributes to recruitment failure. Although a variety of factors affect larval survival, substrate conditions in particular could exert both direct and indirect effects. For example, increased deposition of fines would decrease both benthic food supply and the availability of cover habitat (Wood and Armitage 1997; Osmundson et al. 2002; Finstad et al. 2007). Contaminant effects on the survival of benthic invertebrates (Fairchild et al. 2012) might also contribute to food limitations. Carry-over effects (i.e., reduced growth and survival) due to habitat conditions experienced by yolksac larvae provide another potential substrate-mediated effect on the survival of feeding larvae (Boucher 2012). Diminished subsequent growth has also been detected in response to degraded substrates (Chapter 4; Boucher 2012; Crossman and Hildebrand 2012) and

indirectly may decrease survival due to larval size effects (Werner and Gilliam 1984; Fuiman 2002). Although substrate-mediated effects are compatible with both apparent mechanisms at the upstream Waneta site and site-specific data for the ROOS stock, a more definitive diagnosis for this stock requires further investigation. In particular, indicators of larval quality (Ferron and Legget 1994) may provide a potential means to identify whether larval morbidity is increased due to conditions experienced by yolk sac larvae or whether mortality primarily results from effects on feeding larvae.

While habitats occupied by the WAN and ROOS stocks each have well-studied spawning sites, both contemporary and historical spawning locations are less certain for the HLK stock. A portion of this stock spawns at Revelstoke, and those fish residing downstream of Hugh Keenleyside Dam may now spawn either in ALGS tailrace or at Waneta. Currently, substrates in the Revelstoke spawning reach are highly embedded (Tiley 2006) and have been experimentally shown to limit larval hiding (Crossman and Hildebrand 2012) and likely survival (see Chapters 4 and 5). Reservoir backwatering effects and upstream flow regulation provide a possible explanation for increased armouring and embeddedness at that location (see Crossman and Hildebrand 2012). Contemporary movements during the spawning period also suggest fish from the HLK stock may spawn at Waneta (Golder 2006b; Howell and McLellan 2007, 2009). Habitat limitations at that site are discussed above.

The recently identified spawning site in the ALGS tailrace (Terraquatic Resource Management 2011) likely represents the spawning location used in lieu of upstream movement to a historical spawning location. Although spawning was not detected in this reach prior to the construction of the ALGS in 2002 (R. L. & L. 1994), eggs and yolk sac larvae (but only one feeding larvae) were detected in 2010 and 2011 (Terraquatic Resource Management 2011). Based on results in Chapter 4, the large cobble boulder substrate in the tailrace appears to create interstitial habitats that are too large for hiding yolk sac larvae (Chapter 4; Terraquatic Resource Management 2011). The upstream proximity of

ALGS suggests that interstitial infilling may be limited at this location, and as a result modification of the available substrate at this location may provide a long-term option for habitat restoration.

Biological insights and implications for restoration

The presence of demographic differences and historical reproductive isolation (Nelson and McAdam 2012) between spatially-distinct groups of white sturgeon in the UCR are two principal indicators of stock differentiation (Waples and Gagliotti 2006; Reiss et al. 2009). However, while biological evidence supports the historical presence of stocks, this information is relatively recent and management is still based on the assumption of a single homogenous population. Evaluations of the recruitment patterns of assumed aggregate population (the ALL group) show that it has a more complex decline pattern than its four component stocks, and that a stepped decline is indicated for all aging accuracy scenarios. While patterns for this group clearly reflect the decline patterns of component groups, the diagnosis of recruitment failure causation is challenging without considering stock structure. Comparison with the timing of major development projects shows the first decline step coincides with the completion of Hugh Keenleyside Dam and associated changes caused by river regulation. The second decline step is also conceivably a response to river regulation, and could be associated with the completion of Mica and Libby dams. Alternatively, the second decline step could be part of a gradual decline initiated about the time of HKD completion. Unfortunately none of these possibilities identify causal mechanisms.

Retrospective evaluation of recruitment failure based on the ALL groups, and without reference to stocks, provides a much less confident diagnosis because it precludes comparisons based on spatial differences (i.e., the location of the HLK stock upstream of smelter inputs) and temporal differences (i.e., the later timing of the WAN stock decline). While collapse patterns are still definitive for some hypotheses, both nutrient limitations and geomorphological change are indicated as plausible while

both flow and turbidity effects are considered unlikely based only on the removal criterion. These four hypotheses are the same as the list identified by professional judgment (Gregory and Long 2008), which underscores the importance of considering stock structure.

The less definitive identification of recruitment failure causation and the increased probability of misdiagnosis when considering a single aggregated population further emphasize the importance of considering stocks as the appropriate scale of analysis. Although failure to detect significant differences using DNA microsatellites (Drauch-Schrier et al. 2011) may be interpreted as an absence of stock structure, that interpretation is akin to accepting the null hypothesis of no difference. Such an interpretation fails to acknowledge that both mtDNA (Nelson and McAdam 2012) and demography (present results; Van Poorten and McAdam 2010) are leading indicators of differentiation (Zink and Barrowclough 2009), and both show evidence of stock structure. While dams are generally assumed to fragment populations of sturgeon (Jager et al. 2001), the transboundary reach appears somewhat unique as river regulation has apparently led to the concentration of distinct stocks. The need to differentiate between operational and biological definitions of management units is a general problem in fisheries (Reiss et al. 2009), and in the present case evaluation at the level of stocks provides a more defensible approach. Failure to recognize such differences can lead to elevated extinction risk to smaller component stocks (e.g., the BRL stock), and, particularly for endangered species, biological definitions of management units provide a more precautionary approach (Begg et al. 1999).

Demographic differences between groups of fish showing spatial discrete habitat use further indicate that stock structure is still present in the now-modified habitats of the UCR. Identification of demographic and genetic distinctions among groups also conforms to the identification of discrete genetic units associated with distinct spawning locations for lake sturgeon (Welsh et al. 2008). While sturgeon are capable of moving throughout the transboundary reach (Golder 2006b; Howell and

McLellan 2011; Nelson and McAdam 2012), the maintenance of demographic distinctions for over thirty years shows a very high level of habitat fidelity. This finding has important implications because sustained demographic differences suggest that restoration affecting one stock (e.g., at one spawning site) may have limited benefit for other stocks, particularly the HLK and WAN stocks which show no demographic connections. Restoration at multiple spawning sites may therefore be needed in order to maintain the current distribution and biological diversity of white sturgeon in UCR. Additionally, the identification of finer-scale ordering within lake sturgeon spawning sites (Forsythe et al. 2012) suggests that restoration of only a portion of a spawning site may limit restoration effectiveness from both genetic and demographic perspectives.

Although the present analysis successfully identified putative causal mechanisms of the historical recruitment failure in the UCR, it is important to note that subsequent anthropogenic effects may also limit restoration. While geomorphological change provides a sufficient explanation for recruitment failure, restoration may require more than simply reversing this condition. For example, subsequent construction of Revelstoke Dam, which led to hypolimnetic withdrawal from the upstream reservoir, has substantially decreased summer temperatures (Tiley 2006), leading to effects such as delayed spawning and development (Golder 2006d; Crossman and Hildebrand 2012). Growth of early juveniles is also slower than in the transboundary reach (James Crossman, BC Hydro, pers. comm.), suggesting temperature and nutrients may both affect early growth, and possibly survival. It is therefore uncertain whether substrate restoration leading to increased larval survival will be sufficient to restore recruitment within Arrow Lakes Reservoir.

Identification of changes to spawning substrates as the apparent cause of recruitment collapse adds to a growing list of studies that identify the importance of substrate condition at sturgeon spawning sites (see Kerr et al. 2010; Du et al. 2011). The positive implication of this finding is that

restoration may be more spatially restricted than when large-scale drift is assumed to require whole river restoration (e.g., Kynard et al. 2002; Braaten et al. 2008, 2012). The delayed recruitment decline of the WAN stock also emphasizes the importance of tributary effects in the conservation of riverine fish (Moyle and Mount 2007). The sustained demographic difference between two roughly sympatric groups presents a possible analog for recruitment differences between pallid sturgeon (*Scaphirhynchus albus*) and shovelnose sturgeon (*Scaphirhynchus platorhynchus*), which suggests that recruitment collapse of pallid sturgeon may result from mainstem impacts, whereas the absence of recruitment failure for the smaller shovelnose sturgeon may suggest that they spawn in tributaries (see Pracheil et al. 2009). Differentiation between mainstem and tributary spawning stocks also provides interesting insight because tributary spawning groups (e.g., WAN stock, Willamette River - Chapman and Jones 2011) may form distinct stocks within a possible metapopulation structure.

Table 3.1 Timing of major industrial projects affecting the upper Columbia River watershed. For hydroelectric dams, small (S) and large (SS) storage projects are identified to indicate the project's potential to affect seasonal flows.

Watershed / Industry	Dams / impact	Timing
Columbia mainstem / Hydroelectric dams and reservoirs	Grand Coulee (SS) Hugh Keenleyside (SS) Revelstoke Mica (SS)	1944 1968 1983 1974
Kootenay / Hydroelectric dams and reservoirs	Brilliant Canal Plant Duncan (S) Libby (SS) Lower/upper Bonnington, South Slocan/Corra Linn (S)	1944 1975 1969 1972 1907 - 1932
Pend d'Oreille / Hydroelectric dams and reservoirs	Waneta Seven Mile Boundary Box Canyon/ Albeni Falls (S) / Noxon Rapids / Cabinet Gorge / Hungry Horse (S) /Kerr (S) /Thompson Falls/Priest Lake (S)	1954 1979 1967 1915 -1960
Columbia mainstem / Lead Zinc smelter (Trail)	Contaminants release Slag release	1910-present; significant declines after 1995 1910-1994
Columbia mainstem / Pulp mill (Castlegar)	Contaminants	1961-present; declined significantly after 1993

Table 3.2 Description of the recruitment failure hypotheses evaluated based on the expected pattern of effect on recruitment.

Hypothesis	Description of Mechanism
Overfishing	In conjunction with low intrinsic population growth rates, recruitment failure could occur if harvest diminished populations below threshold levels, for example via Allee effects.
Flow regulation	Recruitment failure is a direct result of flow regulation via effects such as decreased spawning flows, hydraulic effects on spawning site selection or increased predation due to diminished water velocities.
Connectivity	Prior to impoundment, white sturgeon could move throughout the UCR. Recruitment failure may have occurred as a direct result of a decreased ability to move to their requisite habitats.
Contaminants	The UCR is affected by contaminants from a variety of sources (e.g., lead zinc smelter, pulp mill, municipal effluent). The presence of contaminants may have caused the recruitment failure through direct toxicological effects.
Geomorphic change	Sediment supply and river bed disruption due to flow regulation and long-term slag inputs may all contribute to geomorphic change. Recruitment failure may be caused by resultant habitat changes, particularly an increase in the proportion of fine material in river bed substrates at spawning sites.
Habitat diversity	Dams, reservoirs and flow regulation may have decreased the diversity of riverine habitats (e.g., side channels, off channel rearing areas), and the loss or alteration of such habitats may have led to recruitment failure.
Total gas pressure (TGP)	Elevated TGP in the UCR downstream of Keenleyside Dam may have caused recruitment failure by increasing mortality, particularly for larvae and juveniles.
Turbidity	Turbidity decreases downstream of large reservoirs may lead to recruitment failure via increased predation mortality due to increased water clarity.
Nutrients and food supply	Nutrient reductions due to nutrient trapping by upstream reservoirs could lead to a decrease ecosystem productivity. Such changes could cause recruitment failure via effects such as decreased spawning frequency and decreased early life history survival.
Temperature	Temperature increases in the UCR have occurred due to upstream impoundment and possibly climate change.
Altered fish species composition	Changes in the community composition include the loss of anadromous salmonids and increased exotic species (e.g., walleye, northern pike smallmouth bass), and the effects of such changes are poorly understood. Recruitment failure could occur if changes in fish community composition increased predation mortality.

Table 3.4 Scoring criteria used to describe apparent recruitment patterns that would result due to impacts from different recruitment failure hypotheses.

Criteria	Category – Rationale
Temporal lag (WAN vs. ROOS /- WAN)	Would the hypothesized impact mechanism lead to later effects for the WAN group compared to the downstream ROOS group (Yes/No)
Collapse phase pattern	Binary – an irreversible change from one state to another, with very limited range overlap expected (e.g., connectivity related to dam construction)
	Variable – the range of impact magnitude is similar, but the distribution with its range has changed (e.g., an increased frequency of high water temperature)
	Positive – the impact severity has declined and risk due to this variable has decreased relative to the time of recruitment failure (e.g., overharvest, inputs of some contaminants)
Life stage affected	Adult, juvenile, early life history (ELH)

Table 3.3 Estimated timing of recruitment failure for three aging inaccuracy scenarios. Values in brackets are the 5% and 95% confidence intervals (i.e., 67 = 1967). AD indicates results when four additional years of zero recruitment were assumed. NS= not significant (exp *F*, *p* > 0.05).

Group	No inaccuracy	Low inaccuracy	High inaccuracy
HLK	1968 (67-72)	1967 (66- 71)	1951 (50-55)
	1972 (71-74)		
BRL	NS	NS	1949 (44-60)
WAN	1978 (77-80)	1977 (76 – 81)	1972 (71 -77)
ROOS	1973 (72- 77)	1968 (67 – 74)	1959 (57 –68)
ALL	1969 (68-74)	1967 (66-72)	1958 (57-62)
	AD=1969 (68-78)		
		1977 (76-79)	1972 (71-74)
	AD= 1978 (77-80)		

Table 3.5 Weighted comparisons for the retrospective evaluation of recruitment failure hypotheses. Criteria and scoring are described in the methods. Comparisons that refuted hypotheses are indicated by R. For evaluation of the collapse phase, expected recruitment patterns were identified as positive (P), binary (B) or variable (V) recruitment. For the relative differences between stocks, whether an impact mechanism was waterborne (W) or the location of impacts (L) is indicated.

Hypothesis	Temporal Correlation					Spatial Correlation				Relative difference	Coherence				
	HLK (+1/ -3)	WAN (+1/ -3)	ROOS (+1/ -3)	ALL (+1/ -3)	Collapse phase pattern	HLK (+1/ -3)	WAN (+1/ -3)	ROOS (+1/ -3)	ALL (+1/ -3)		Theoretical (+2/ -2)	Factual (+2/ -3)	Biological (+2/ -2)	Life stage (+2 / -2)	Removal (+2/ -2)
Over-harvest	0	0	0	0	-2 (P)	0	0	0	0	1 (L)	-3	-3	0	-2	-2
Flow regulation	1	1	1	1	-1 (V)	1	1	1	1	-3 (W)	2	0	0	2	-1
Connectivity	1	-2	1	-2	1 (B)	1	R	R	-3	-3 (W,L)	2	R	0	-2	0
Contaminants:															
-Pulp mill	-1	-2	-1	-1	-1 (P)	-1	1	1	1	R (W)	2	0	-2	2	-2
-Smelter	-3	-3	-3	-3	-1 (P)	-2	1	1	-1	-3 (W,L)	2	-1	2	2	-1
Geomorphological change	0	0	1	0	1 (B)	1	1	1	1	1	2	2	2	2	2
Habitat diversity	1	-2	-2	-1	1 (B)	1	-3	1	1	-3 (W)	2	-2	0	2	0
Gas supersaturation	1	-1	1	1	-3 (V/P)	-2	1	1	1	R (W)	2	0	2	2	-2
Turbidity	-1	-1	-1	-1	-1 (V)	1	1	1	1	-3 (W)	2	0	2	2	-1
Nutrients and food supply	1	-1	1	1	1 (B)	1	1	1	1	-3 (W,L)	2	1	0	2	0
Temperature	1	-1	1	1	-3 (V)	1	1	1	1	-3 (W,L)	2	1	2	2	-2
Fish species composition	-1	-2	-1	-1	1 (B)	-1	1	1	1	-2 (L)	2	1	1	2	0

Table 3.6 Summary of the scoring rationale for recruitment failure hypotheses. Signs in parentheses indicate whether evidence supports (+) or does not support (-) each hypothesis.

Hypothesis	Determination	Rationale
Overharvest	Unlikely	<ol style="list-style-type: none"> 1. Should affect juveniles and adults (-) 2. Allee effects unsupported (-)
Flow regulation	Unlikely	<ol style="list-style-type: none"> 1. Mainstem flow regulation does not explain later decline of the WAN stock (-) 2. Flow regulation on the Pend d'Oreille River preceded recruitment failure (-) 3. High flow in 1997 only led to low level recruitment (+)
Connectivity	Refuted	<ol style="list-style-type: none"> 1. Should primarily affect HLK stock and fish in Arrow Lakes Reservoir. (-) 2. ROOS and WAN stocks show limited movement to the vicinity of Hugh Keenleyside Dam (-) 3. HLK stock fish are still spawning at locations upstream and downstream of Hugh Keenleyside Dam (-) 4. Cannot explain the later decline of the WAN stock (-)
Contaminants	Unlikely	<ol style="list-style-type: none"> 1. The two major contaminant sources preceded recruitment failure by eight years (pulp mill) or 55 years (smelter) (-) 2. Most contaminants (except slag) are waterborne and cannot explain the later recruitment failure of the WAN stock (-) 3. Contaminants from the smelter are located downstream from the primary habitat of the HLK stock (-) 4. Contaminant levels from both sources have decreased substantially, but with no recruitment effect (-) 5. Toxicological studies show exposure to Ca, Cu and Zn are detrimental, but only at levels above current ambient concentrations (-) 6. Tissue sampling and summary investigation found no clear evidence of contaminant mediated recruitment effects (-) 7. Contaminant levels were higher historically (+) 8. Benthic invertebrate survival diminished (+)
Geomorphic change	Likely	<ol style="list-style-type: none"> 1. Can explain the later decline of the WAN stock (+) 2. Substrates are embedded at all spawning sites (except the ALGS site which is recently created) (+) 3. Drift by yolk sac larvae at all spawning sites indicates an inability to access interstitial habitat (+) 4. Substrates that limit hiding by yolk sac larvae are linked to recruitment failure in other sturgeon (+) 5. Timing of putative mechanism agrees with recruitment failure timing (+)
Habitat diversity	Unlikely	<ol style="list-style-type: none"> 1. Off-channel habitat was historically limited in the transboundary reach and was minimally affected by flow regulation (-) 2. Off-channel habitat was reduced by the creation of Lake Roosevelt, but over 25 years prior to recruitment failure (-) 3. Losses of off-channel habitat near Revelstoke coincided with the timing of recruitment failure and the creation of Arrow Lakes Reservoir (+)

Table 3.6 Summary of the scoring rationale for recruitment failure hypotheses (cont.)

Hypothesis	Determination	Rationale
Total gas pressure (TGP)	Refuted	<ol style="list-style-type: none"> 1. TGP was elevated seasonally, but not in all years (-) 2. TGP levels have declined substantially (-) 3. Elevated TGP is a waterborne effect and cannot explain the later recruitment failure of the WAN stock (-) 4. White sturgeon larvae typically reside below the compensation depth (-) 5. Lab studies show elevated TGP can be lethal (+)
Turbidity	Unlikely	<ol style="list-style-type: none"> 1. Historical turbidity levels were not high (-) 2. Turbidity levels declined after recruitment failure (-) 3. Historically peak turbidity levels occur during non-freshet periods (-) 4. Turbidity is a waterborne effect and cannot explain the later recruitment failure of the WAN stock (-) 5. Laboratory studies show that elevated turbidity can decrease predation, but only at levels higher than ambient or historical conditions (+)
Nutrients and food supply	Unlikely	<ol style="list-style-type: none"> 1. Nutrient levels show complex response to reservoir formation. 2. Initial increases followed by declines would lead to nutrient declines occurring after the initiation of recruitment failure (-) 3. Egg viability suggests adult condition is adequate (-) 4. No evidence of nutrient limitation for HLK and ROOS stocks (-) 5. Lower growth of the WAN stock may limit reproductive frequency (+)
Temperature	Unlikely	<ol style="list-style-type: none"> 1. Temperature is a waterborne effect and cannot explain the later recruitment failure of the WAN stock (-) 2. Temperatures are higher than historically, but are not high every year (-) 3. Temperatures can exceed early life history tolerance limits and mortality at the Waneta spawning site, but effects are intermittent (+)
Altered fish species composition	Unlikely	<ol style="list-style-type: none"> 1. Increased walleye abundance preceded recruitment failure (-) 2. There is no apparent mechanism by which walleye might affect both the HLK and ROOS stocks prior to the WAN stock (-) 3. Laboratory studies do show predation on white sturgeon, but effects on early life history stages are limited (-) 4. Field studies do not show that sturgeon are abundance in walleye stomachs (-) 5. Recruitment failure is present in Arrow Lakes Reservoir in the absence of walleye and other introduced species (-)

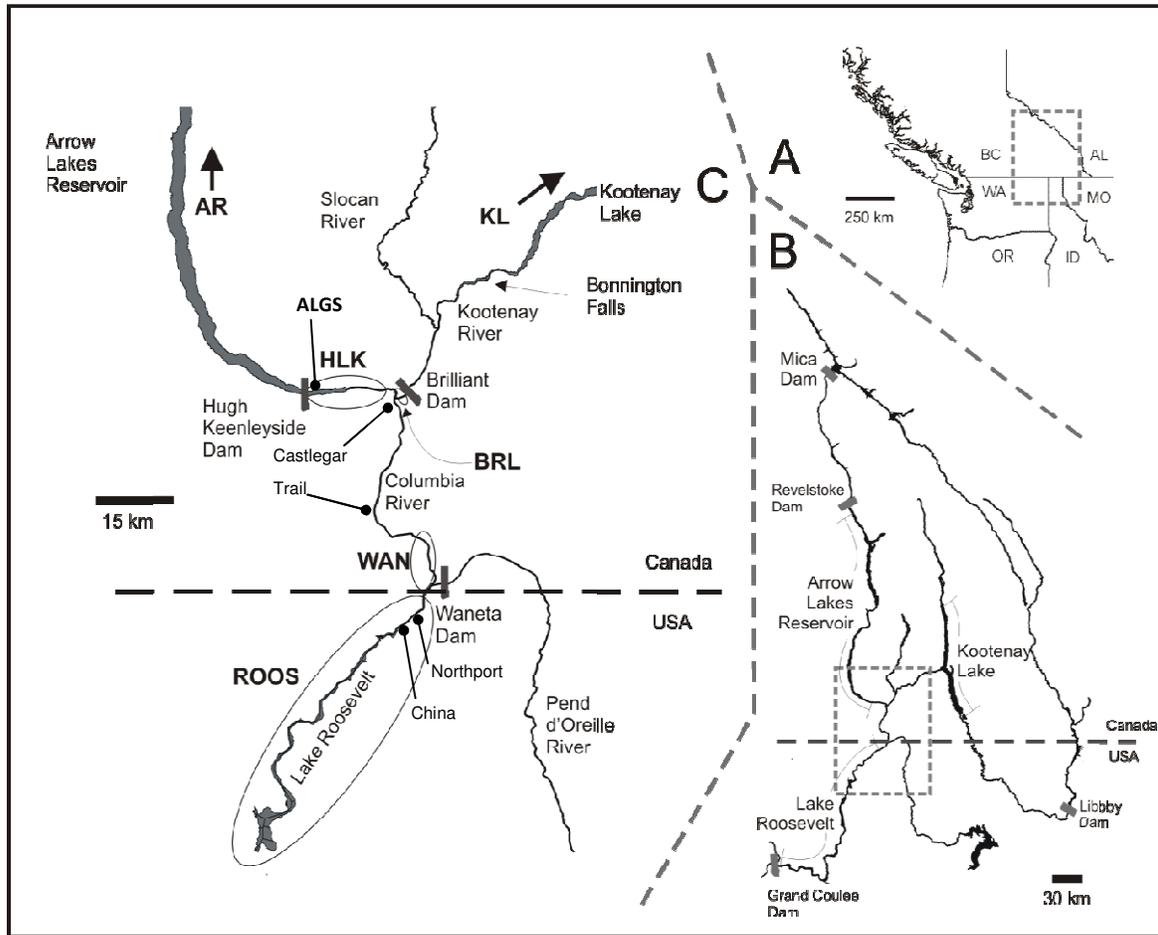


Figure 3.1 Map of the transboundary reach of the upper Columbia River and its relative location on the west coast of North America (A). Geographic groups defined in the text are indicated in bold adjacent to their associated river zone (C). Principal dam locations are indicated by text and curved arrows. Bold abbreviations referring to putative groups of white sturgeon are defined in the text, and include fish in Arrow Lakes Reservoir (AR), directly downstream of Keenleyside Dam (HLK), directly downstream of Brilliant Dam (BRL), the Waneta area (WAN) and Lake Roosevelt (ROOS). Kootenay Lake and the population it contains (KR) are also identified for reference. Adapted from Nelson and McAdam (2012). © Journal of Applied Ichthyology, 2012, adapted by permission.

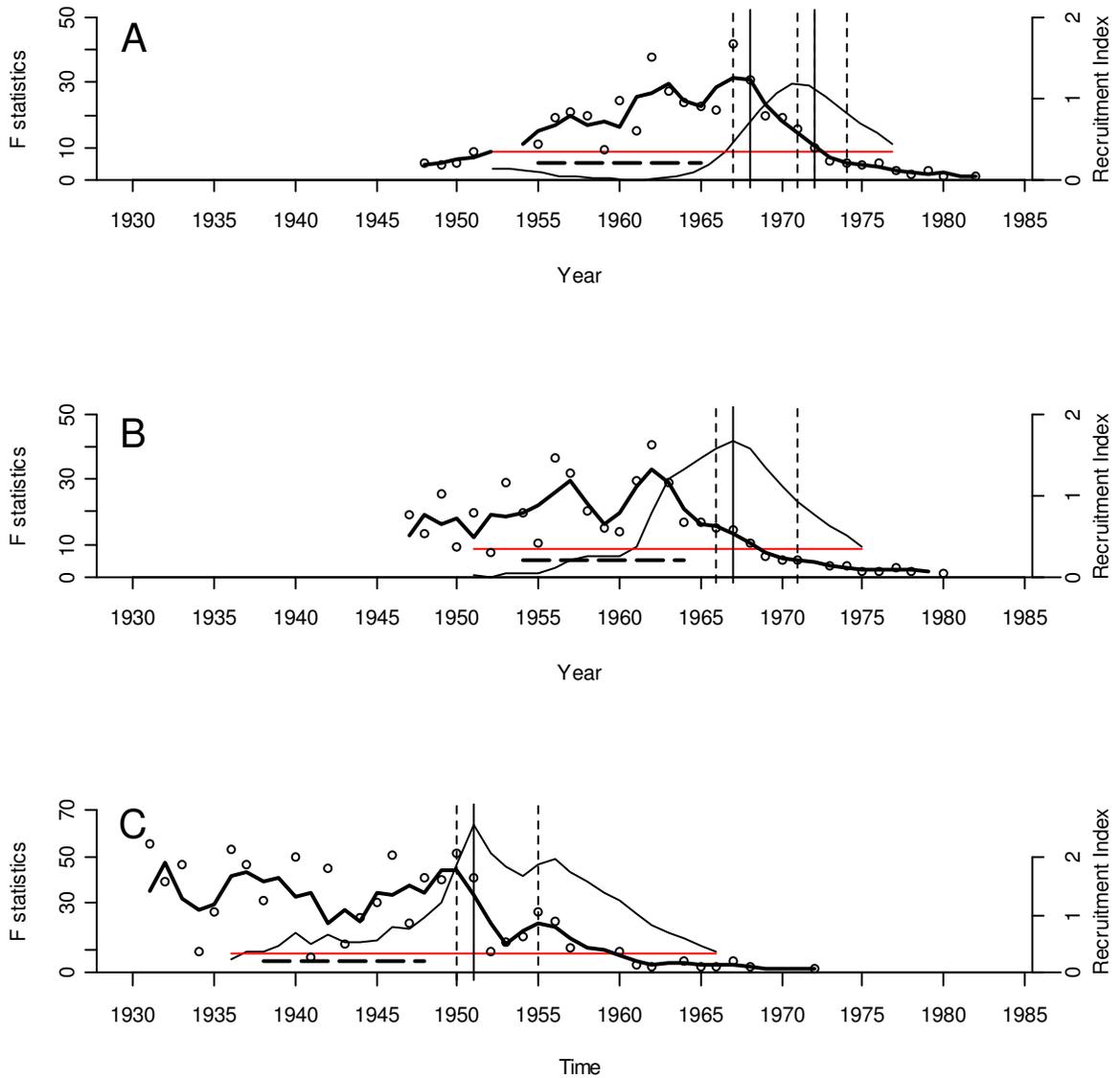


Figure 3.2 Hindcasted recruitment for the HLK stock, including the HLK-N (A), HLK-L (B) and HLK-H (C) aging inaccuracy scenarios (see definitions in methods). The thin black line is the F statistics (left axis) and the red horizontal line indicates the significance level. Solid vertical lines are breakpoints and dashed vertical lines are the 5% and 95% confidence intervals. The bold line is the three-year moving average of annual recruitment (points – right axis). The dashed bold horizontal line indicates the historical reference period.

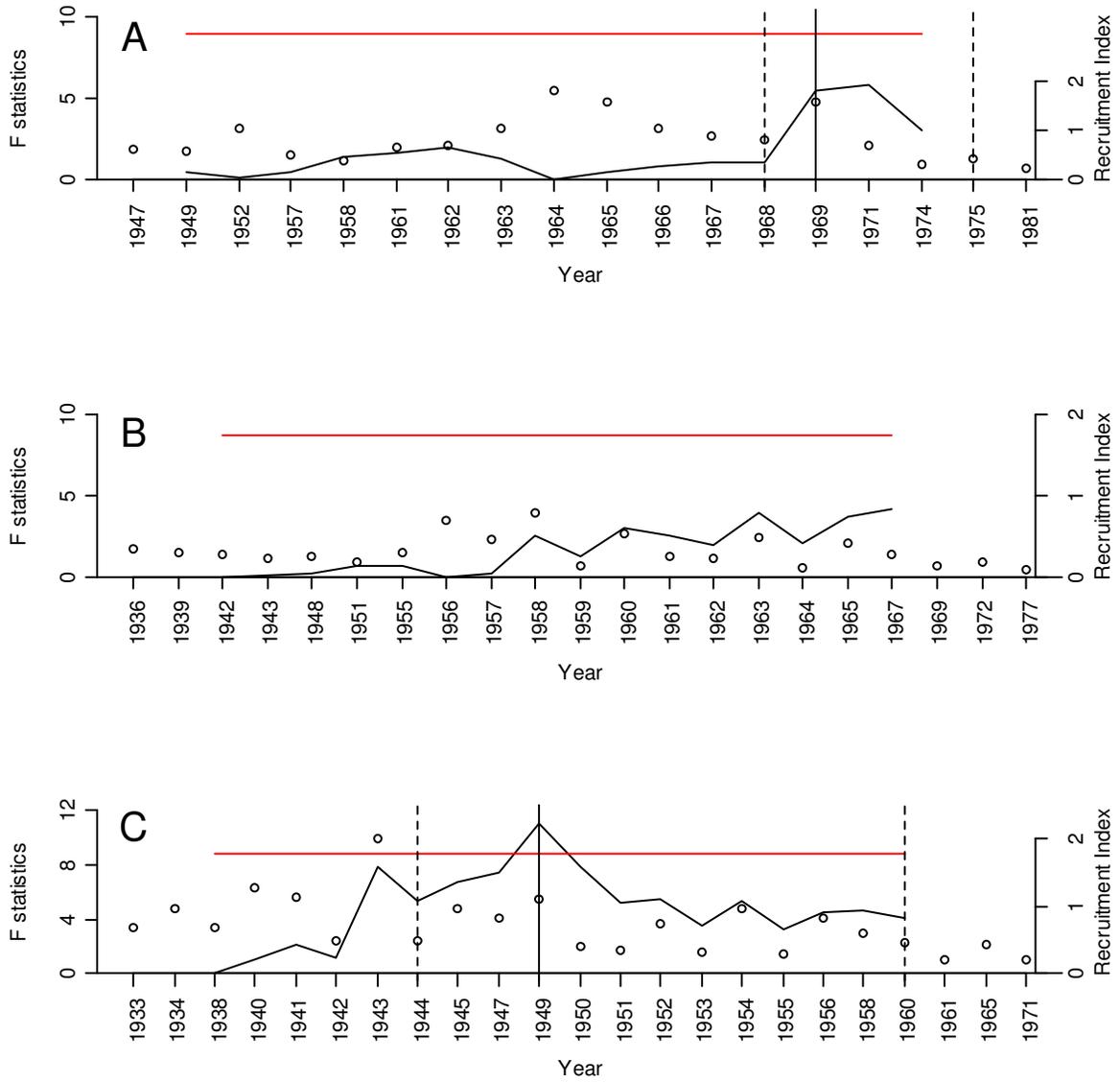


Figure 3.3 Hindcasted recruitment in various years for the BRL stock, including the BRL-N (A), BRL-L (B) and BRL-H (C) scenarios (see definitions in methods). The thin black line is the F statistics (left axis) and the red horizontal line is the significance level. Solid vertical lines are breakpoints and dashed vertical lines are the 5% and 95% confidence intervals. Note that the x-axis is discontinuous and only shows years for which data were available.

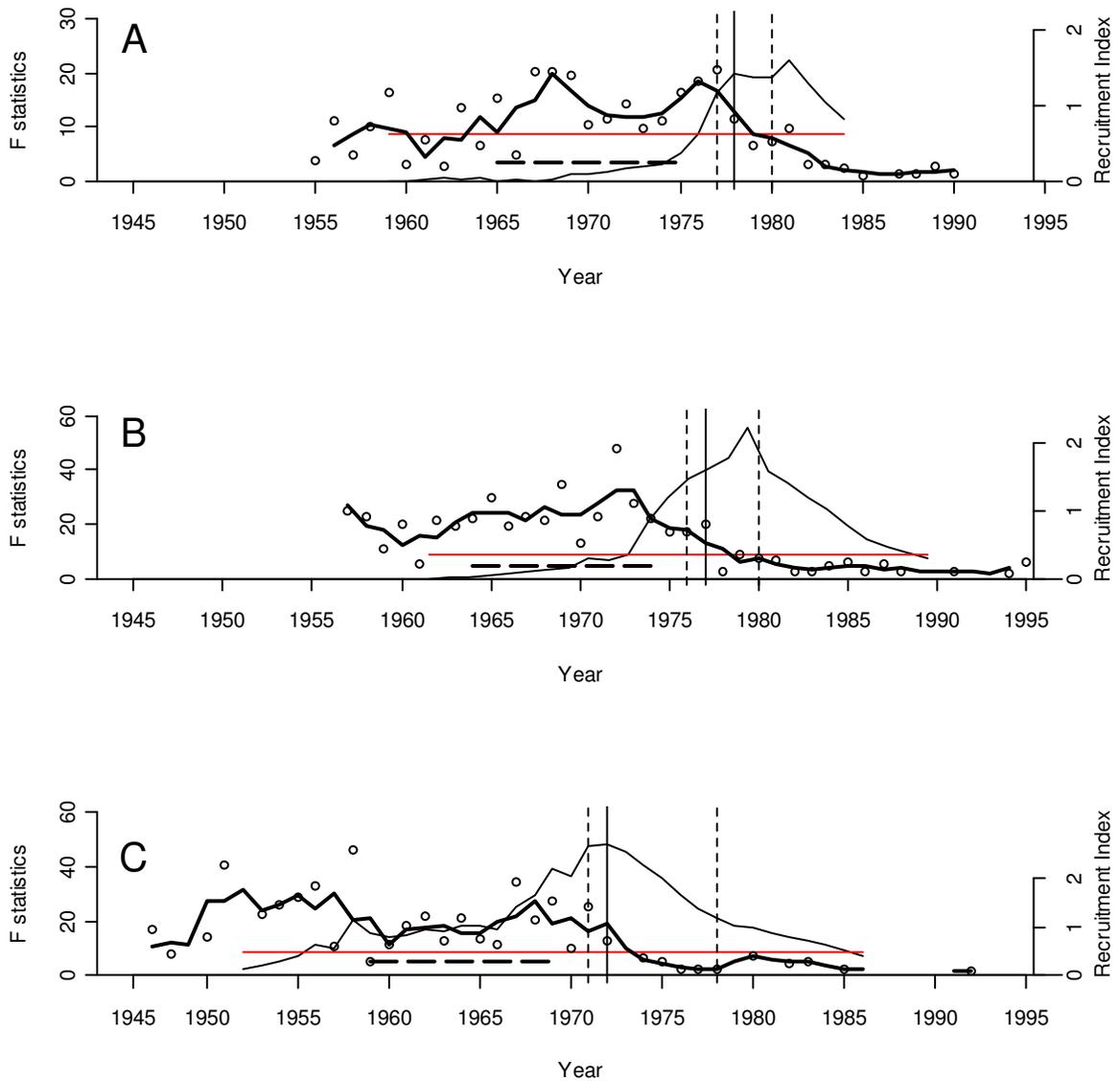


Figure 3.4 Hindcasted recruitment for the WAN stock, including the WAN-N, (A), WAN -L (B) and WAN -H (C) aging inaccuracy scenarios (see definitions in methods). The thin black line is the F statistics (left axis) and the red horizontal line indicates the significance level. Solid vertical lines are breakpoints and dashed vertical lines are the 5% and 95% confidence intervals. The bold line is the three-year moving average of annual recruitment (points – right axis). The dashed bold horizontal line indicates the historical reference period.

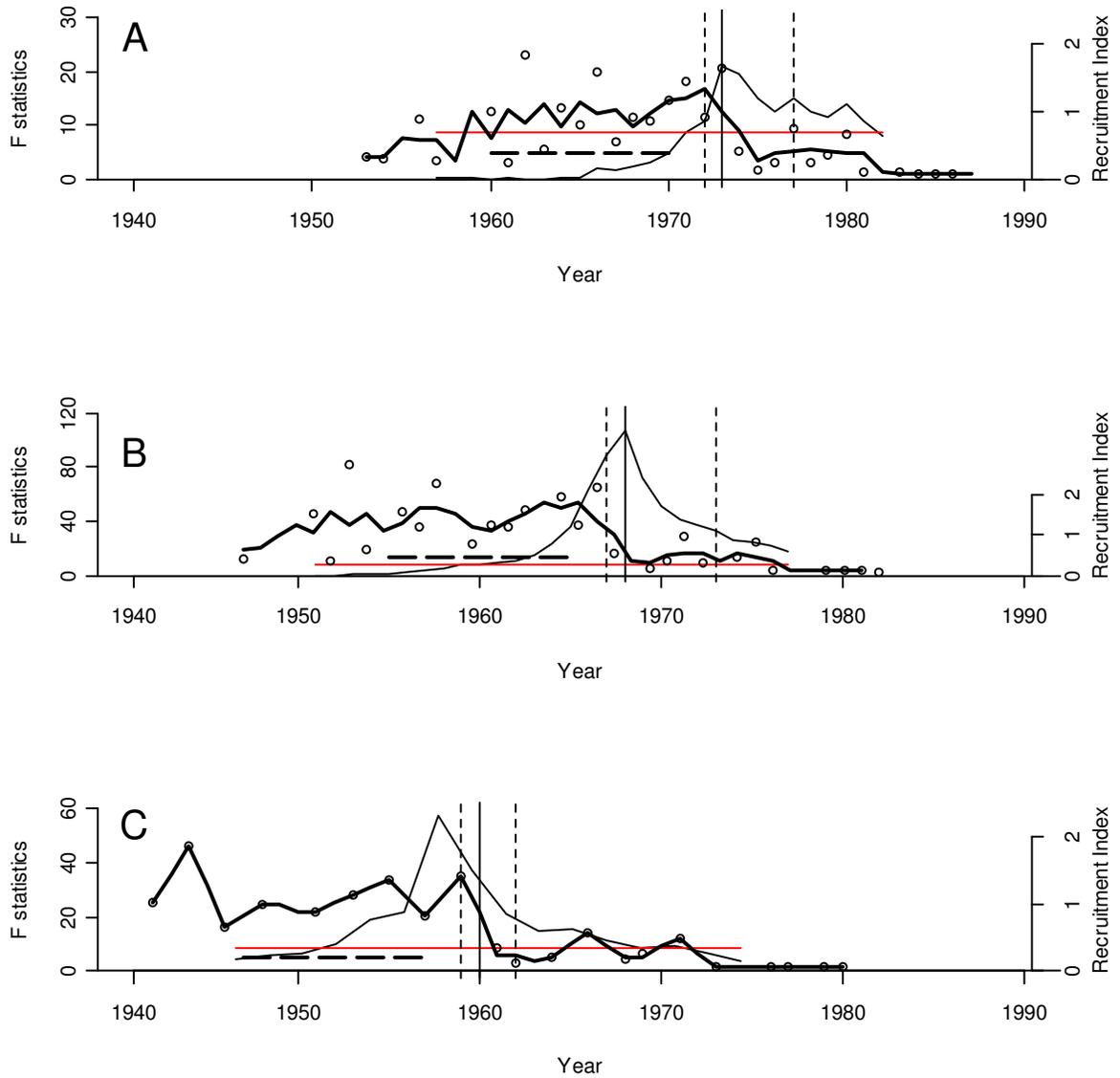


Figure 3.5 Hindcasted recruitment for the ROOS stock, including the ROOS -N, (A), ROOS -L (B) and ROOS -H (C) aging inaccuracy scenarios (see definitions in methods). The thin black line is the F statistics (left axis) and the red horizontal line indicates the significance level. Solid vertical lines are breakpoints and dashed vertical lines are the 5% and 95% confidence intervals. The bold line is the three-year moving average of annual recruitment (points – right axis). The dashed bold horizontal line indicates the historical reference period.

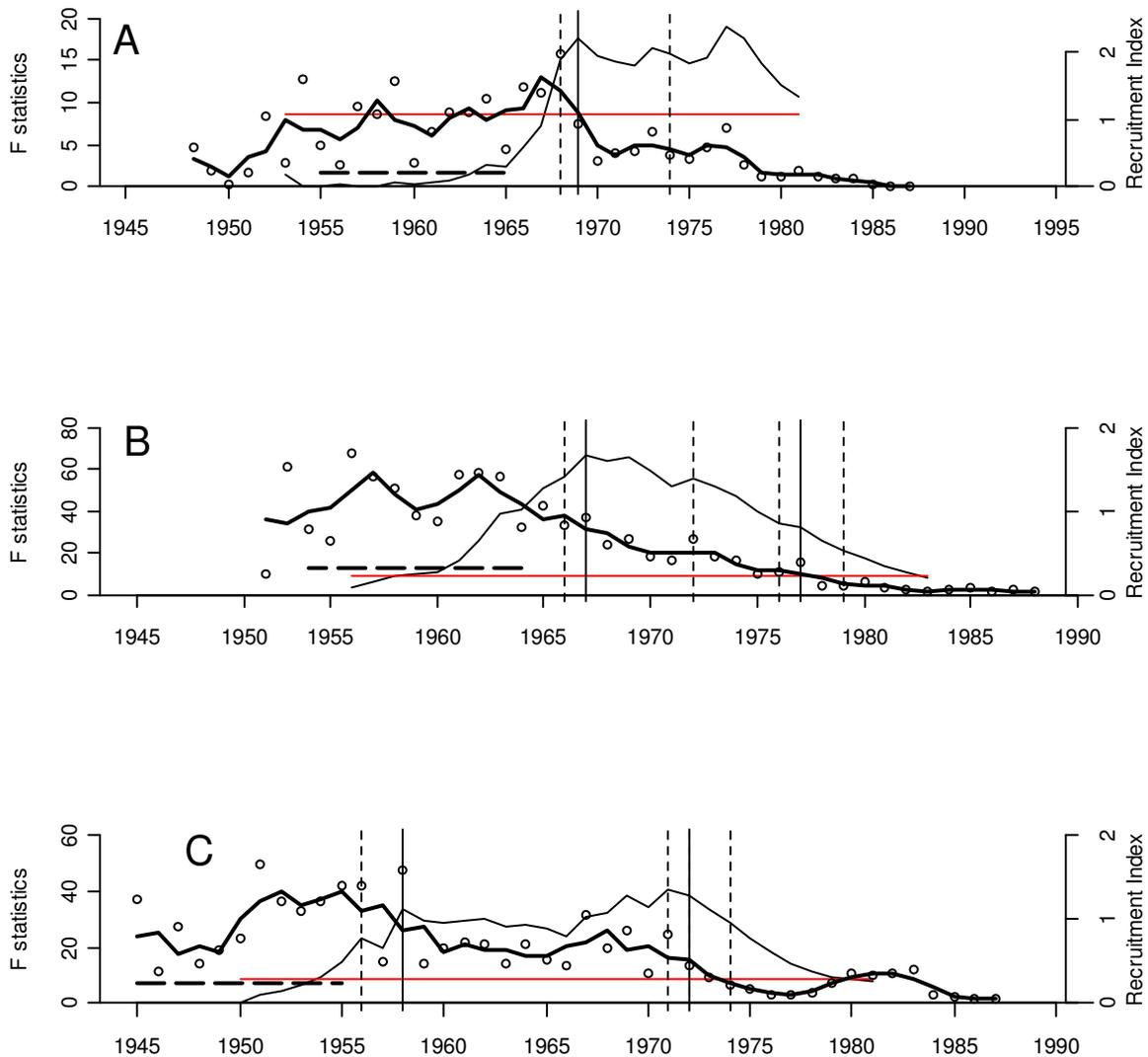


Figure 3.6 Hindcasted recruitment for the ALL stock, including the ALL -N, (A), ALL -L (B) and ALL -H (C) aging inaccuracy scenarios (see definitions in methods). The thin black line is the F statistics (left axis) and the red horizontal line indicates the significance level. Solid vertical lines are breakpoints and dashed vertical lines are the 5% and 95% confidence intervals. The bold line is the three-year moving average of annual recruitment (points – right axis). The dashed bold horizontal line indicates the historical reference period.

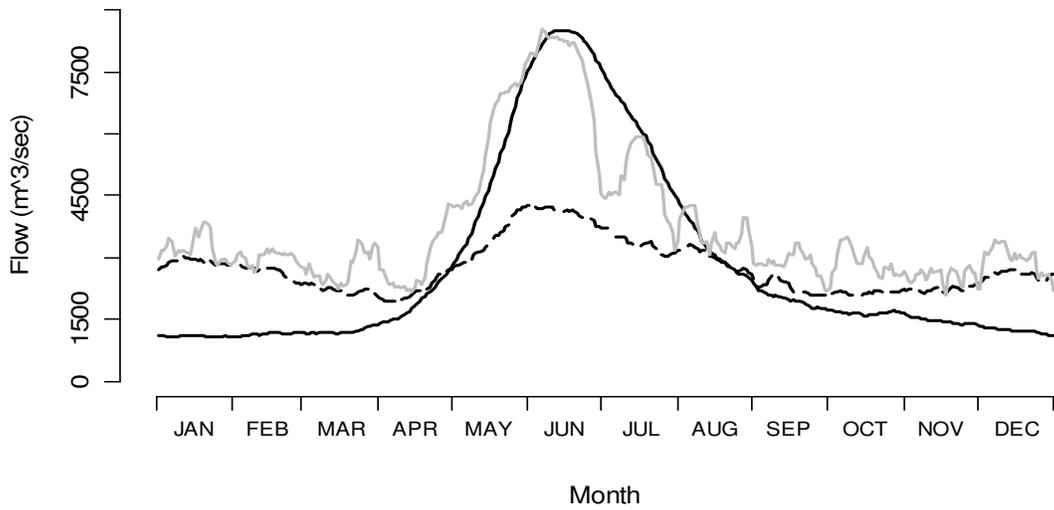


Figure 3.7 Historical and contemporary flow for the Columbia River at the Canada-U.S. border. Mean 1938-68 (solid), mean 1975-2001 (dashed), 1997 (grey). Data provided by BC Hydro.

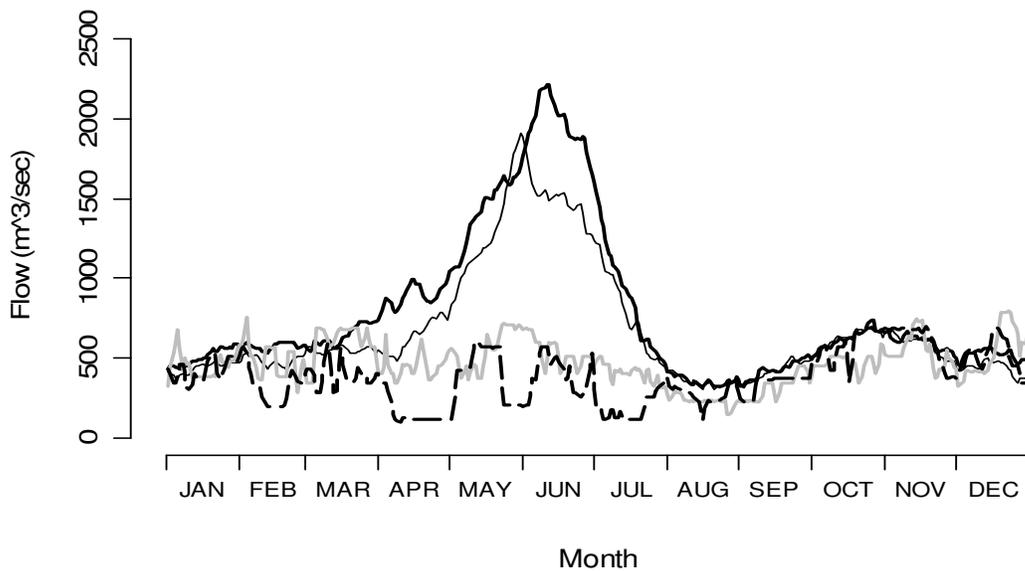


Figure 3.8 Mean and annual flow in the Pend d'Oreille River at Albeni Falls Dam prior to (1966-75 –black, bold) and after (1976-85 – black, thin), apparent changes in freshet volume in 1976. Two years (1973-grey, bold; 1977 -black, dashed) with uncharacteristically low flows are also shown.

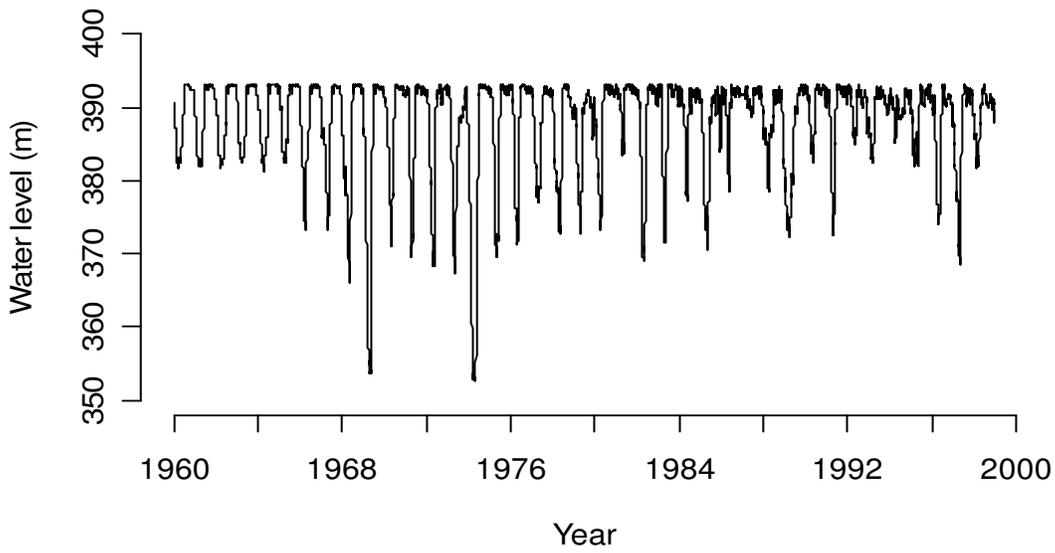


Figure 3.9 Daily elevation (meters above sea level) of Lake Roosevelt from 1960 to 2000.

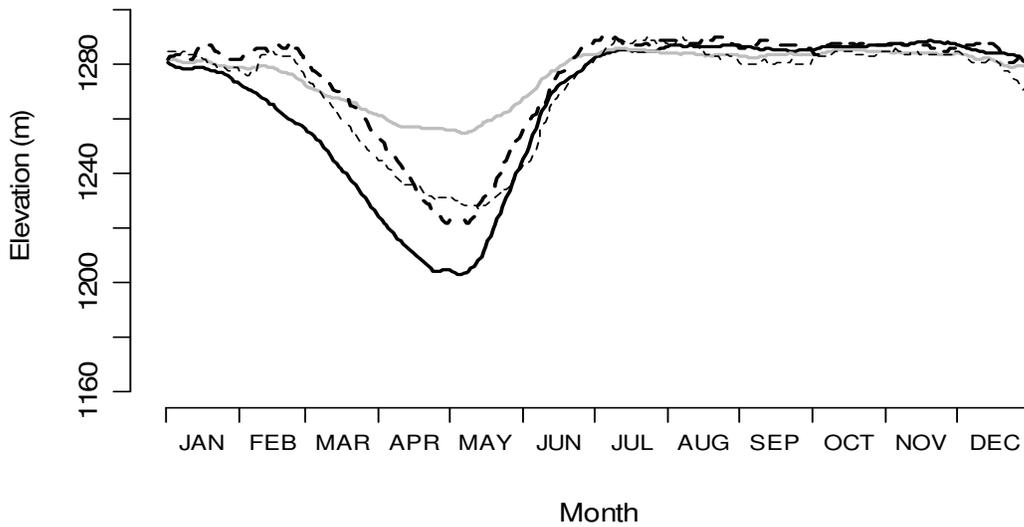


Figure 3.10 Daily elevation (meters above sea level) of Lake Roosevelt prior to (mean 1968-73, solid black) and after (mean 1991-96, grey) management changes about 1980. The years 1991 (bold black, dashed) and 1996 (thin black, dashed) demonstrate that variation similar to the historical conditions is still present from June to December in some years.

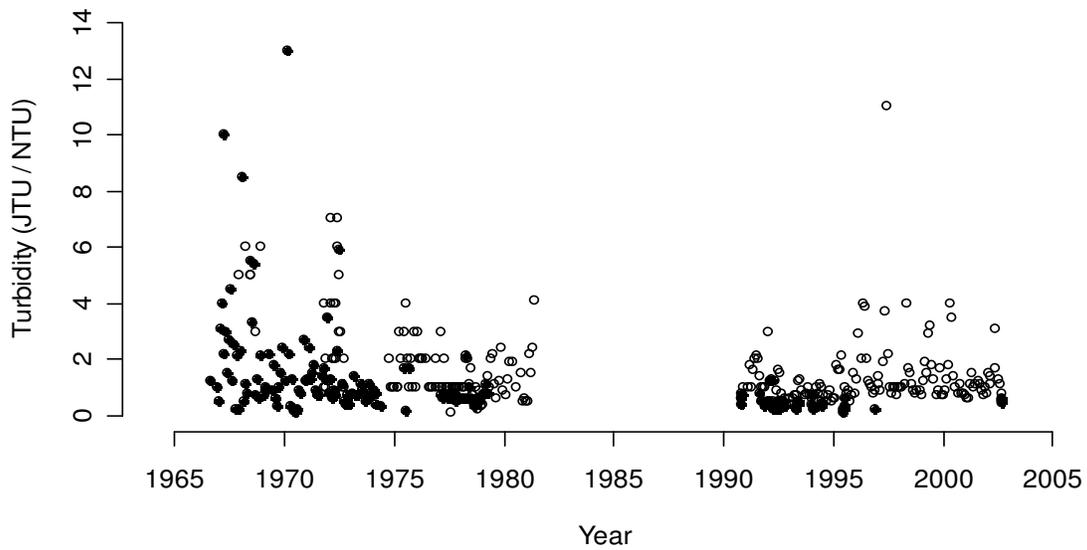


Figure 3.11 Turbidity at Northport (open circles) and Castlegar (filled circles) from 1967 to 2002. Note that Northport data prior to 1975 used Jackson Turbidity Units (JTU), which are roughly equivalent to Nephelometric Turbidty Units (NTU).

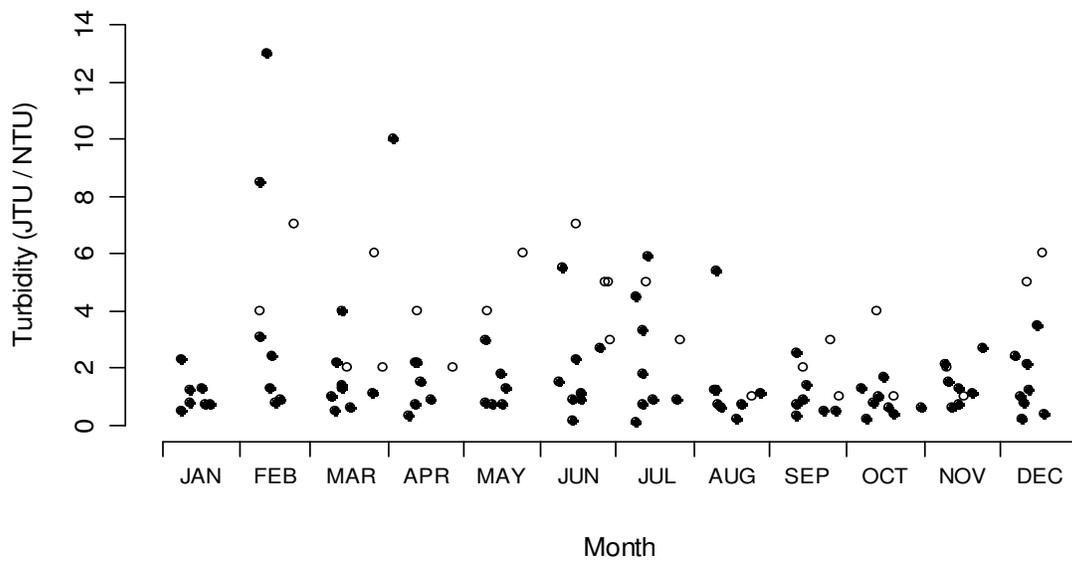


Figure 3.12 Seasonal pattern of turbidity prior to 1974 for Castlegar (filled circles) and Northport (open circles).

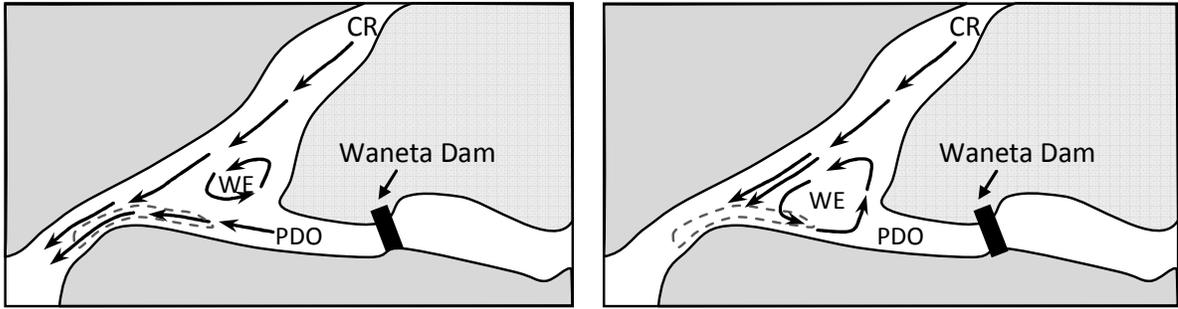


Figure 3.13 Schematic diagram of water circulation patterns at the confluence of the Columbia and Pend d'Oreille Rivers when Waneta Dam output is non-zero (left) and (right) when there is zero turbine or spillway flow (Fissel and Jiang 2007). WE = Waneta Eddy, CR = Columbia River, PDO = Pend d'Oreille River. Dashed grey line indicates the Waneta spawning area.

Chapter 4 Effects of substrate condition on habitat use and survival by white sturgeon (*Acipenser transmontanus*) larvae, and potential implications for recruitment

Introduction

Analysis of hindcasted white sturgeon recruitment for white sturgeon in the Nechako and Columbia rivers (Chapter 2, 3) identified an increase in fine substrates at spawning sites as the probable cause of recruitment failure. In conjunction with the identification of substrate effects for Kootenay River white sturgeon (McDonald et al. 2009), lake sturgeon (Nichols et al. 2004) and Chinese sturgeon (*A. sinensis*; Du et al. 2011), the analyses suggest that sturgeon are part of a group of large-bodied riverine fish whose early life history is affected by sedimentation (e.g., Atlantic salmon (*Salmo salar*)– Peterson and Martin-Robichaud (1995); Colorado pikeminnow (*Ptychocheilus lucius*) – Osmundson et al. (2002); robust redhorse (*Moxostoma robustum*; Jennings et al. (2010)). Substrate change is commonly associated with river regulation and the loss of flushing flows (Rieser et al. 1990), and the presence of dams in most rivers inhabited by sturgeon suggests substrate-mediated impacts may be more common than previously thought (though see Williot et al. 2002; Ruban 2005). However, while the impact of substrate is recognized, the detailed mechanism of its effects through the entire early life history phase is not well understood. This uncertainty is particularly acute for white sturgeon yolksac larvae due to substantial differences among studies in hypothesized behaviour and habitat use during this stage. Investigation of the effects of substrate condition on the behaviour and survival of yolksac larvae could provide important insight into both the mechanisms of substrate-mediated impacts and the potential for habitat restoration.

Survival during early phases including the embryo, yolksac larvae and feeding larvae is a key driver of recruitment for many fishes (Houde 1987), including sturgeon (Gross et al. 2002; Parsley et al. 2002), and the association between recruitment failure and substrate changes suggests that early life

history survival is directly affected by substrate conditions. For white sturgeon, recruitment failure in the Kootenay River has been specifically attributed to high bed load sand movement, leading to the smothering of embryos and mortality (Kock et al. 2006; Paragamian et al. 2009). Yolksac larvae are the oldest larval stage detected in the Nechako River (Triton 2009); however, the presence of feeding larvae as the oldest detectable stage at one spawning site in the upper Columbia River (Howell and McLellan 2007, 2009) suggests that substrate-mediated mortality may affect both larval stages. The identification of a substrate preference only for yolksac larvae (Bennett et al. 2007) suggests that this stage may be particularly prone to the effects of substrate change, with increased predation providing a potential mechanism (Gadomski and Parsley 2005).

Preferred sturgeon spawning habitat typically includes areas of high water velocity with gravel and cobble substrate (Parsley and Beckman 1994; Billard and Leconte 2001). Subsequent to hatching, drift and hiding behaviour have both been observed in laboratory studies, and for white sturgeon yolksac larvae drift has been suggested to last one to six days (Brannon et al. 1985; Deng et al. 2002; Kynard and Parker 2005). However, there are important limitations in these studies of larval behaviour. Most importantly, methodological differences may be the primary reason for contrasting conclusions. For example, studies that observed early hiding of yolksac larvae (Brannon et al. 1985; Kynard and Horgan 2002; Gessner et al. 2009) provided gravel substrate, whereas all studies that observed early dispersal of yolksac larvae (e.g., Zhuang et al. 2003; Kynard et al. 2005) lacked substrate with interstitial spaces. Because even short exposure to high velocities in spawning areas could lead to displacement downstream of important habitats (e.g., the 2 km spawning reach in the Nechako River), early life history habitat use has important implications for understanding the spatial extent of larval habitat and potential links between habitat condition and recruitment limitations.

In the present study, I carried out four laboratory experiments to provide a more detailed understanding of the relationship between substrate condition, habitat use and survival during the early life history of white sturgeon. First, in order to understand the immediate responses of larvae at hatch, I examined whether larvae showed a greater tendency to hide or drift immediately after hatching when exposed to gravel substrates. Second, I investigated the presence of rapid hiding in white sturgeon aged 1, 6, 10 and 15 days post hatching (dph) in response to sand, small gravel, medium gravel, cobble and embedded cobble substrates to test the effect of substrate on larval drift and hiding. Because predation, and not starvation, would be the primary source of mortality for yolk sac larvae, I examined whether substrate condition led to survival differences in the presence of a predator. Finally, in response to the prolonged presence of feeding larvae within augmented gravel habitats in field experiments (Chapter 5), I examined the effect of gravel depth on the retention of feeding larvae. While caution must be exercised when extending laboratory results to natural conditions, my findings are discussed with regard to their potential implications for our understanding of larval sturgeon habitat use, and the potential links between substrate condition and recruitment limitation.

Methods

Larval behaviour at hatch

Investigation of the predominant behaviour immediately after hatching was undertaken by evaluating the proportion of newly-hatched larvae that hid in response to porous substrate. Eight replicate tests were conducted on sequential nights between June 7 and 11, 2007 using embryos from three unique families derived from captive spawning of wild broodstock from the Nechako River. Subsequent to fertilization and neutralization of the adhesion layer using fine clay (according to Conte et al. 1988), embryos were maintained at 15°C in McDonald jars in a streamside hatchery in

Vanderhoof, BC. Tests were conducted in a field lab located adjacent to the hatchery. Water supply for these tests was non-chlorinated Vanderhoof municipal water.

Tests were conducted in two Plexiglas flumes (Figure 4.1). Horizontal baffles in the water intake area at the upstream end of the flumes were used to diminish turbulence. A fine mesh barrier, which further dampened turbulence, separated the upstream end of the flume from the test section. The central section of the flume, the test section, measured 40 x 120 cm (W x L). At the downstream end of the test section, vertical panels were offset, creating a velocity barrier that prevented return upstream movement of larvae that drifted into the collection area. Pumps at the downstream end of the flume circulated water to the upstream end, and were separated from the larval collection area by fine mesh. Water velocity was 4 cm/sec and temperature was maintained between 14 and 16°C.

Treatments were conducted over small gravel substrate (4 cm deep, grain size = 1.2 – 1.9 cm) covering the bottom of the test section. The presence of rapid hiding immediately after hatch was evaluated by placing 80 hatching embryos in a small plastic container (the embryo basket – 12 x 12 cm x 5 cm deep) at the upstream end of the flume test section at 20:00 hrs. The embryo basket had an open top and a perforated bottom through which larvae could pass (but embryos did not). All light sources were then turned off to simulate nocturnal conditions. At 09:00 hrs the next morning lights were turned on, and unhatched eggs and yolk sac larvae in the embryo basket were immediately removed. The number of yolk sac larvae that drifted into the collection area was counted as well as the number and location of yolk sac larvae hiding within substrate in the test section. Results were quantified based on the mean proportion of yolk sac larvae hiding in the test section relative to the total number that left the embryo basket (drift + hide) and the hiding location relative to the release location.

Rapid hiding for age 1 – 15 dph

Behavioural responses of age 1-10 days post-hatch yolk sac larvae and 15 days post-hatch (dph) feeding larvae to five substrates were examined to evaluate whether white sturgeon larval behaviour varied in response to substrate condition. Investigations were conducted at the University of British Columbia (UBC) in June/July 2005 and 2006 and used progeny from the captive spawning of wild broodstock from the upper Columbia River. Embryos were transported from the Kootenay Hatchery (Cranbrook, BC) to Vancouver via air freight and were reared in bare 4 L aquaria containing dechlorinated water and constant aeration. Temperatures in rearing aquaria were held between 14 and 16°C by immersion in a flow through water bath. Larvae from full sibling families (N = 11 families) were maintained in separate rearing aquaria. Feeding was initiated at 12 dph using frozen blood worms (Hikari Bio-Pure) and larvae were fed to satiation three times per day.

Investigation of larval responses to substrate condition at 1, 6, 10 and 15 days post-hatch (dph) was conducted in the same flume design as investigations of larval behaviour at hatch (Figure 4.1). Substrate was present over the entire bottom of the test section, and consisted of either sand (2 cm deep, grain size < 0.2 cm), small gravel (4 cm deep, grain size = 1.2 – 1.9 cm), medium gravel (7 cm deep, grain size = 2.5 - 5.0 cm), cobble (2 layers, grain size = 10.0 - 15.0 cm) or embedded cobble (1 layer of cobble with sand filling $\frac{3}{4}$ the height of cobble grains). Velocities were maintained at 4 cm/sec or 20 cm/sec using submersible pumps, but only small gravel, medium gravel and cobble were examined in the high-velocity treatment. Water depth over substrates was maintained at 17 cm for all tests, and temperatures were maintained within 0.5°C of those in the rearing aquaria. Tests were conducted under subdued light (~4 lux) to represent conditions near the bottom of deep or turbid rivers and because larval drift may be nocturnal (e.g., Kynard and Parker 2005).

Each test was initiated by placing five larvae into 200 mL of water in a covered opaque plastic vial and then inverting the covered vial and resting it on the substrate at the upstream end of the test section. After a two minute acclimation period larvae were released by lifting the vial off the cover, taking care to release fish near the substrate. A minimum of four replicates for each substrate / age combination were tested, except for medium gravel at 1 dph, for which only two replicates were conducted.

Downstream movement out of the test section (drift) was monitored by removing and counting all larvae present in the collection area at two minute intervals for ten minutes. Following test completion, the room lights were turned fully on, and any non-hiding larvae present in the test section were removed with a small net, and their location recorded. Larvae hiding within substrates were located and captured using hand movements to create a 'jet' of water that disturbed surface substrates. In most cases this stimulated larval movement and allowed larvae to be captured. In some cases, and particularly for medium gravel and cobble, substrates were removed in order to ensure that all larvae were captured after each test. Because substrate disturbance limited the detection of hiding location in some cases, uncertain locations were not recorded. Responses were quantified based on the number of larvae that drifted into the collection area and the location of larvae that remained in the test section (hiding and non-hiding) relative to the release location.

Effects of substrate on predation of larval sturgeon

In order to evaluate whether substrate condition affects the level of predation mortality, white sturgeon larvae were exposed to predators in the presence of five different substrate treatments. Both prickly sculpin (*Cottus asper*) and coastrange sculpin (*C. aleuticus*) were used as predators because both are sympatric with white sturgeon and have similar diets (Brown et al. 1995). Preliminary tests also showed that both readily consume white sturgeon larvae. Sculpins collected from the wild were kept in

individual tanks maintained at 16°C by immersion in a water bath, and covered with 0.15 mm thick black plastic to maintain low light levels. Sculpins were fed small goldfish, but no food was provided for 24 hours prior to use in predation tests. Water quality was maintained using activated carbon filters and water was changed every three days. Each rearing tank contained a hollow black plastic tube and several pieces of cobble for cover.

Tests were conducted in June 2006 in 30 x 150 cm (W x L) sections of Plexiglas raceways enclosed with fine mesh at each end (the test arena). Substrate treatments and depth were the same as described for investigations of rapid hiding. Water temperature was maintained within 0.5°C of larval rearing tanks, and varied from 14 to 16°C. Water depth was 20 cm in all tests, and water velocities were zero in order to avoid larval impingement on screens. Tests tanks were covered with 0.15 mm black plastic to maintain light levels < 4 lux and emulate near-bottom conditions in a river. The acquisition and husbandry of white sturgeon used in these tests is the same as described for the investigation of rapid hiding for aged 1-15 dph larvae.

In all trials, one large (mean weight \pm SD = 15.0 \pm 1.5 g, n = 9) and one small (mean weight \pm SD = 6.9 \pm 1.2 g, n = 8) sculpin were used. Individual sculpins were used more than once, but with a minimum one day interval between uses. The testing regime began by placing predators into the test arena in a screened container. Five larvae were then added to the test arena and allowed to acclimate for 30 minutes, after which sculpins were released. Sculpins were removed after 45 minutes and the remaining larvae were counted. Substrate was removed and rinsed to ensure all surviving larvae were detected. A minimum of four replicates was used except at 10 dph, when only two or three replicates could be completed.

Effects of gravel depth on larval drift

The detection of feeding larvae within augmented gravel substrates in the field experiment after the age at which drift was expected (Chapter 5) led to the hypothesis that excessive gravel depth leads to larval entrapment and prevents drift. A laboratory experiment was therefore undertaken to test that hypothesis. Larvae procurement and embryo rearing were the same as described above, although tests were undertaken in 2008.

The effects of gravel depth on larval drift were investigated using oval raceways (10 cm x 20 cm x 70 cm – W x D x L) that contained gravel depths of 2, 6 and 10 cm (gravel size 1.2 cm-1.9 cm). Four replicates were conducted for each depth. Aquaria were maintained within an environment chamber and temperatures were between 14 to 18°C and a photoperiod of 16L/8D. Water velocity within each tank was 4 cm/sec and was maintained by an external pump. Water quality was maintained by daily changes of half the water in each aquarium. Seventy larvae each from three distinct families (total = 210) were placed into each raceway at 1 dph.

Larval drift was monitored by sampling the full area of the raceway cross section using a vertically-oriented net to capture drifting larvae. Nets were initially placed in the tanks for the duration of the eight hour night phase (scotophase); however, once larvae were detected, sampling was intensified and nets were retrieved every two hours throughout scotophase. At 11 dph nets were again sampled only at the end of scotophase, after which the experiment was terminated and live and dead larvae remaining in the substrate were counted.

Data analysis

Statistical analysis was conducted using procedures and recommendations provided in Zar (1984), with an assumed $\alpha = 0.05$ for all tests. Data regarding drift distances and the effects of gravel depth were analyzed by ANOVA followed by Tukey tests. Data from all rapid hiding and predation

experiments were treated as counts, and were square root transformed ($x^2+0.5$) prior to applying t-tests or ANOVA. Data for the evaluation of behaviour immediately post hatch were treated as proportions and were arcsine transformed prior to applying a t-test.

Results

Larval behaviour at hatch

Of the 80 embryos included in each of eight replicate tests, just over half (42 ± 21 (mean \pm SD)) hatched, although 13 ± 16 of the hatched larvae remained within the embryo basket. Of the 236 yolk sac larvae that left the embryo basket, the majority ($67 \pm 17\%$, $n=8$) hid within substrates rather than drifting downstream (t-test, $p < 0.01$). The mean hiding location downstream of the hatching basket was 52.7 cm ($n=150$) (Figure 4.2). Assuming larvae moved downstream at ambient water velocities, this mean location implies that larvae hid an average of 13.3 seconds after leaving the embryo basket.

Investigation of rapid hiding for age 1-15 dph

The behaviour of larvae during ten minute tests at 4 cm/sec led to clear differences in the larval drift responses between substrates with and without interstitial hiding habitat at 1 dph (ANOVA, $p < 0.001$) and 6 dph (ANOVA, $p < 0.001$), but not at 10 dph ($P = 0.089$) or 15 dph ($P = 0.10$) (Figure 4.3). At 1 dph all five larvae drifted through the test section for all replicates when exposed to sand or embedded cobble (non-porous substrates). Considering all porous substrates at 1 dph together, an average (\pm SD) of 3.5 ± 1.4 larvae remained in the test section and all hid within the substrate. At 6 and 10 dph, larvae that remained in the test section when exposed to sand showed improved swimming and were located either in small irregularities in the substrate or the flume structure (e.g., micro eddies at the corner of the upstream screen). By contrast, all larvae that remained in the test section in porous substrate treatments hid within substrate interstices at 6 dph and 10 dph. Embedded cobble

showed high drift at all ages, apparently due to the lower abundance of microhabitat features where larvae could hide. At 15 dph the mean number of drifting larvae after ten minutes varied from 3.6 ± 1.5 (cobble) to 5 ± 0 (sand, small gravel) and there was no apparent difference between substrates (Figure 4.3).

Sequential sampling at two minute intervals showed that clear behavioural distinctions are apparent within the first two minutes of testing. This pattern was best shown at 1 dph at low velocity, when mean drift in the first two minutes was 76 to 80% of mean total drift after ten minutes for sand and embedded cobble treatments versus 20 to 40% for porous substrates (Figure 4.4).

Tests at 20 cm/sec generally showed increased drift relative to lower velocities and, with the exception of 1 dph larvae over small gravel (mean drift \pm SD = 1.2 ± 1.2), all other treatments exceeded the mean of 3.0 ± 1.5 drifting larvae shown by small gravel at 6 dph (Figure 4.5). The significant difference (two tailed t-test, $p = 0.011$) between 1 dph larvae exposed to small gravel and cobble (mean \pm SD = 3.6 ± 1.3) coupled with the lack of difference at other ages indicates that the strongest behavioural hiding response is present at 1 dph and the small gravel provides a better interstitial hiding habitat than cobble.

Hiding locations of larval sturgeon were regularly and reliably detected only in small gravel, because other substrates had to be removed to locate larvae, which led to uncertainty in hiding location. For small gravel substrates in low-velocity tests, the mean distances between release location and hiding location were 22.0 cm and 25.5 cm at 1 and 6 dph, respectively; the distance increased significantly to 50.6 cm at 10 dph (ANOVA, $p < 0.001$) (Figure 4.2). The mean distances to hiding locations for high-velocity treatments were 40 cm, 37 cm and 54 cm for these same three ages respectively; no significant difference was shown with age. In the small gravel treatment, all larvae

drifted at 15 dph for both velocity treatments. At 1 dph larvae hid within 5.5 seconds and 2.0 seconds after release for water velocities of 4 cm/sec and 20 cm/sec respectively (Figure 4.2).

Effects of substrate on predation on larvae

Exposure to predation by sculpins led to clear differences between treatments at 1 dph based on comparison of the maximum survival for a non-porous substrate of $16\% \pm 16\%$ (mean \pm SD) versus a minimum for any porous substrate of $56\% \pm 26\%$ (ANOVA, $p < 0.01$) (Figure 4.6). Sand substrates led to all larvae being consumed at all ages, except 6 dph when a mean of $3.2\% \pm 8.2\%$ of larvae survived. Although the small gravel treatment consistently showed the highest survival at all ages, there were no significant treatment effects at 6 dph (ANOVA, $P = 0.053$), 10 dph (ANOVA, $P = 0.39$) or 15 dph (ANOVA, $P = 0.57$) (Figure 4.6).

Effects of gravel depth on larval drift

Investigation of the effects of gravel depth on larval drift showed decreased total drift with increased gravel depth, but the timing of drift was similar for all groups. Drift was first detected at 7 dph in 2 cm and 6 cm gravel depth treatments (Figure 4.7). Peaks in larval drift occurred two hours after the initiation of darkness for all groups, with a subsequent increase at the end of scotophase for the 6 cm treatment. The mean total number (\pm SD) of drift-caught larvae retrieved was 194 ± 6 , 160 ± 20 , and 129 ± 21 for the 2 cm, 6 cm and 10 cm treatments, respectively, but only the 2 cm treatment was significantly different (ANOVA $p < 0.01$, Tukey test $p < 0.05$). After removal of gravel, the mean (\pm SD) number of live larvae recovered for the 2 cm, 6 cm and 10 cm treatments respectively were 13 ± 4 , 40 ± 17 and 58 ± 23 . Although there were significant differences (ANOVA, $p < 0.05$), treatment differences were not resolved by the Tukey test ($p > 0.05$). The number of mortalities was 1 ± 0.5 , 2 ± 2 and 6 ± 2 , for the 2 cm, 6 cm and 10 cm treatments, and only the 10 cm treatment was significantly different (ANOVA, $p < 0.01$; Tukey test, $p < 0.05$).

Discussion

Larval sturgeon behaviour

Like most other Acipenseridae, the white sturgeon is a conservation concern throughout its geographic range, and recruitment is a concern for many populations. In extreme cases, chronic recruitment failure means some white sturgeon populations face certain extirpation without intervention (Wood et al. 2007), and uncertainty regarding the mechanisms that cause recruitment failure continues to limit recovery action. Because spawning is regularly observed (e.g., Howell and McLellan 2007, 2009; Triton 2009) and viable eggs are produced, explanations for recruitment failure have been sought in early life history survival. Correlations between river flow during the early ontogeny period and recruitment (e.g., Shaw et al. 2012) also suggest the importance of early life history survival to recruitment (Nilo et al. 1997). Based on a range-wide analysis of white sturgeon recruitment, Coutant (2004) suggested that a loss of flooded riparian habitat may be the underlying cause of recruitment failure. However, evidence from the Nechako and upper Columbia rivers (Chapters 2, 3) indicates that lost riparian habitat may not provide the best explanation, and suggests that recruitment failure may result from increased fine substrates within main channel benthic habitats (Chapter 2,3; Paragamian et al. 2009).

Benthic habitat use and interstitial hiding have been identified previously for white sturgeon yolksac larvae (Brannon et al. 1983, 1985), although prior studies also identified a drift phase from 1-6 dph (Brannon et al. 1985; Deng 2002; Kynard and Parker 2005). Dispersal by early yolksac larvae has been suggested for many sturgeon species (Zhuang et al. 2003; Kynard and Parker 2005; Kynard et al. 2005, Braaten et al. 2008, 2012), but the prevalence of hiding when porous substrates are available (present results; Richmond and Kynard 1995; Gessner et al. 2009) suggests that observation of a prolonged drift phase by early yolksac larvae may be an artefact of substrate conditions. This “hide or

drift” dichotomy that has apparently resulted from methodological differences between past studies has significant implications because these two distinct behaviours lead to very different perceptions of habitat use, which has created confusion about links between habitat and recruitment. For example, based on observations of yolksac larvae drift in both lab (Kynard et al. 2002) and field (Braaten et al. 2008, 2012), pallid sturgeon have been suggested to have an obligate drift phase that requires over 300 km of continuous fluvial habitat (Kynard et al. 2002; Braaten et al. 2008, 2012). By comparison, Kempinger (1988) showed that capture of yolksac larvae was restricted to about 250 m downstream of spawning sites for lake sturgeon where cobble substrates apparently provided suitable hiding habitat.

In my experiments, the comparison of short-term behaviour between substrate treatments showed that most age 1 to 6 dph yolksac larvae hid when exposed to porous substrates at 4 cm/sec, whereas nearly all larvae drifted in response to non-porous substrates. At 20 cm/sec significantly lower drift was only observed at 1 dph over small gravel. These results clearly indicate that substrate condition affects drift behaviour, and that hiding is the primary behaviour of white sturgeon when suitable interstitial habitat is available. Furthermore, examination of behavioural responses immediately after hatching shows that the hiding response is initiated immediately. My results therefore support the suggestion that the dichotomy between prior observations of drift (Zhuang et al. 2003; Kynard and Parker 2005; Kynard et al. 2005) or hiding (Richmond and Kynard 1995; Kynard and Horgan 2002; Gessner et al. 2009) by early yolksac larvae is likely due to differences in whether or not substrate was provided and differences in the nature of the substrate among experiments. The suggestion that early dispersal may be adaptive (e.g., Kynard and Horgan 2002; Kynard and Parker 2005) therefore appears premature because this inference was based on studies lacking suitable hiding substrate. In contrast, my data suggest that the behavioural responses of larval sturgeon are more complex, and are critically dependant on ambient substrate and flow conditions. While this suggestion

must be confirmed for other sturgeon species, the present analysis suggests that hiding throughout the yolk sac larval period may be more common than previously considered.

At 15 dph, consistent with the general tendency for increased drift at the initiation of exogenous feeding in sturgeon (e.g., Auer and Baker 2006; Gessner et al. 2009), no significant difference was observed between treatments; there was high drift for all substrates at both water velocities. In contrast, the non-significant difference at 10 dph in low-velocity tests resulted in part from decreased drift over sand substrates due to improved larval swimming ability, which allowed larvae to limit downstream drift. (While the peak of larval drift in the gravel depth experiments occurred earlier than 10 dph, the higher rearing temperature would have led to more rapid development in that experiment.) The increased standard deviation in drift for all substrates at 10 dph and the significant increase in the distance between release and hiding locations may also reflect an increase in larval swimming ability relative to younger ages. Drift results in the short-term experiments at 10 dph demonstrate that ontogenetic changes in swimming capability can also affect larval drift in laboratory studies conducted at low velocities irrespective of substrate condition, and this effect would increase with larval age. However, similar effects might not be expected under field conditions due to the potential for higher velocities.

Given that the importance of substrate for yolk sac larvae has only recently been emphasized, the effects of gravel depth on larval behaviour have not been previously examined in sturgeon. Larval drift peaked in early scotophase for all gravel depth treatments, which clearly indicates that drift by feeding larvae is nocturnal, and both nocturnal drift and the early scotophase peak in drift (Auer and Baker 2002) have been observed in field studies of white sturgeon (Chapter 5; Crossman and Hildebrand 2012) and lake sturgeon (Auer and Baker 2002). Although the detection of peak larval drift at 8 dph

was earlier than suggested based on the short duration tests discussed above, that is likely due to the higher rearing temperature in the study of gravel depth effects (16 to 18°C).

The significantly greater number of larvae that drifted when gravel depths were only 2 cm indicates that larval entrapment prevented larvae in the deeper gravel treatments from emerging. The similarity in peak drift timing for all gravel depths suggests that the detected drift response is primarily due to larvae that hid near the substrate surface (e.g., those within 2 cm of the gravel surface). The presence of a secondary drift peak near the end of scotophase for the 6 cm treatment at 7 dph and 8 dph may therefore reflect the emergence of larvae that resided on the tank bottom within the 6 cm treatment. If so, this suggests that emerging larvae are capable of upward movement through gravel at about 1 cm/hr. However, it is important to note that the present study was based on smaller substrates than are typically associated with sturgeon spawning habitat, and therefore the interstitial pore size may be smaller than larvae would experience naturally. The use of larger grain sizes for habitat restoration (see Kerr et al. 2010) may also limit such effects in restored habitats.

Habitat and behaviour of larval sturgeon

The consistent identification of hiding and survival responses for white sturgeon yolk sac larvae suggests small interstitial spaces provide important habitat at this life stage (cf. Bennett et al. 2007 who identified a preferred substrate size). Significantly higher drift over cobble relative to small gravel at 1 dph and 20 cm/sec indicates that larger interstitial spaces are not preferred hiding places, even in the presence of two layers of contiguous substrate. Although the uniform substrates examined here may not reflect the mixture of substrate grain sizes expected under natural conditions, the observed preference for small interstitial spaces would presumably be met by mixed substrates expected to occur within and beneath preferred spawning substrates.

Gravel-cobble substrates are an important component of preferred spawning habitat for many sturgeon species (Parsley and Beckman 1994; Billard and Lecointre 2001). For Atlantic sturgeon, Gessner et al. (2009) showed that 75% of yolk sac larvae at 22 hours post hatch hid within five minutes, which agrees with the present observations. Examination of hiding locations from hatch to 6 dph demonstrates that hiding occurs within 2 to 13.3 seconds, indicating that hiding is essentially immediate at these ages when substrate is suitable. Greater survival of interstitial lake sturgeon embryos as compared to those on substrate surfaces (Johnson et al. 2006; Forsythe 2010) suggests that most embryos may also hatch interstitially. Immediate hiding after hatching therefore suggests that yolk sac larvae predominantly hide in the immediate vicinity of the spawning area. While larval hiding at spawning locations has been previously suggested (Richmond and Kynard 1995), the failure to identify it as a broader phenomenon in sturgeon is an apparent outcome of laboratory studies that failed to stimulate hiding behaviour due to an absence of suitable substrates (e.g., Gisbert and Williot 1997; Kynard et al. 2002; Zhuang et al. 2003). By contrast, the provision of substrates that elicit the full behavioural repertoire of sturgeon strongly suggests that the hiding of yolk sac larvae should be localized in the vicinity of spawning sites.

Larval drift is widely observed in riverine fish (e.g., Johnston et al. 1995; Humphries and Lake 2000); however, the present results emphasize the importance of changes in drift behaviour for different larval stages (see Urho 2002). Drift is generally assumed to allow movement from incubation habitat to nursery (feeding) grounds (Fuiman and Werner 2002); however, the presence of exogenous yolk reserves in sturgeon yolk sac larvae may diminish the need to drift at this stage, instead allowing larvae to deal with their other main ontogenetic problem besides food, namely predation risk. Furthermore, limited sensory and locomotory capabilities at this stage (Loew and Sillman 1998; Urho 2002; Muller 2008), coupled with predation risk of even short exposure to predators (this study; Gadowski and Parsley 2005), suggests that downstream dispersal creates a high risk of increased

mortality, either during drift or due to settlement in lower-quality habitat. For white sturgeon, because spawning habitats should also provide hiding habitat, drift by yolksac larvae would represent a departure from preferred hiding habitat, with no clearly demonstrated benefit. The suggested pattern of a localized distribution of eggs and yolksac larvae in preferred spawning habitat, followed by drift of feeding larvae at the onset of exogenous feeding, is consistent both with present findings and with empirical field data for lake sturgeon (Kempinger 1988, Auer and Baker 2006).

While observed behaviour indicates the potential for rapid hiding by yolksac larvae, it is the survival consequences of behavioural responses to substrate condition that potentially affect recruitment. The presence of significantly higher survival in response to porous substrates (Gotceitas and Brown 1993; Johnson et al. 2006; Jennings et al. 2009), but only at 1 dph, supports the previous suggestion that hiding responses may be strongest for early yolksac larvae. The combination of a rapid hiding response and high predation mortality in the absence of interstitial habitat also indicates that substrate changes may exert their most critical effect shortly after embryos hatch. For example, larvae that cannot hide due to an absence of interstitial habitat would face substantially increased predation-induced mortality, and if habitat changes are sufficiently strong, these effects could conceivably lead to 100% mortality shortly after hatch. This suggests that larval access to interstitial habitats may be fundamental to survival, and while laboratory experiments are overly simplified relative to natural conditions, they do suggest that increases in predation mortality of yolksac larvae may be sufficient to create recruitment failure. The identification of behavioural and survival effects of fine substrates adds white sturgeon the list of species negatively affected by fine substrates as a result of altered habitat use (Finstad et al. 2007) and decreased survival (Olson and Peterson 1986; Heggenes 1988; Jennings et al. 2010). The hypothesized links between substrate change and population level recruitment failure (Chapter 3, 4; Paragamian et al. 2009) suggest sturgeon may be particularly prone to such effects,

possibly due to fact that they do not modify spawning substrates as compared to some other riverine fishes (Jennings et al. 2010), particularly salmonids (Gottesfeld et al. 2004).

Implications for habitat restoration and conservation in sturgeon

While laboratory experiments provide the opportunity for both manipulative studies and more detailed behavioural observations, it is important to emphasize that field verification of observed patterns is required to fully understand what behaviours may manifest under more natural conditions. Bearing this in mind, the present analysis suggests that detection of drifting sturgeon yolksac larvae in rivers may reflect habitat conditions that limit hiding. For example, the detection of drifting yolksac larvae, but not feeding larvae, downstream of spawning sites utilized by populations undergoing recruitment failure (e.g., the Nechako River - Triton 2009; the upper Columbia River – Golder 2005a, 2006a, 2010; Howell and McLellan 2009, 2011) likely reflects the degraded habitat conditions at those sites (Golder 2006a; Northwest Hydraulics 2008; Triton 2009; Jason McLellan, Colville Tribes, pers. comm.). The detection of primarily newly-hatched yolksac larvae in the tailrace of the Arrow Lakes Generating Station near Castlegar, BC (see Chapter 3; Terraquatic Resource Management 2011) was also attributed to the presence of only large boulder substrates in that newly-created habitat. In that case, the results in this chapter suggest that interstitial habitats created by boulders are much too large to provide yolksac larvae with effective hiding habitat.

In conjunction with the suggestion that egg inundation by fine substrates leads to recruitment failure in the Kootenay River (Paragamian et al. 2009), results from the present studies and field studies (Howell and McLellan 2007, 2009; Triton 2009; Terraquatic Resources Management 2011) suggest that substrate changes may lead to a gradient of recruitment responses. The most severe habitat alterations may be present in the Kootenay River, because the near absence of yolksac larvae (Duke et al. 1999) indicates nearly complete mortality during the embryo phase. The detection of drifting

yolksac larvae as the oldest detectable stage in association with other spawning sites (e.g., Nechako – Triton 2009; Waneta – Golder 2005a, 2010; Revelstoke – Golder 2006) may be indicative of less severe habitat impacts. The detection of both drifting yolksac and feeding larvae downstream of spawning habitats near the Northport Washington on the upper Columbia River therefore may reflect the least severe level of habitat degradation because larvae clearly survive to the feeding larvae stage; however, recruitment failure still affects that stock (Chapter 3; Howell and McLellan 2011). Although stage specific larval drift data are limited for other sturgeon, such a response gradient suggests the detection of drifting beluga sturgeon yolksac larvae (Raspopov and Novikova 1997) may also be indicate of substrate limitations in the Volga River.

Fortunately, there is a fairly substantial history of substrate restoration for increasing early life history survival in salmonids that may provide important insights (e.g., Palm et al. 2007), and an increasing number of successful examples for sturgeon. While substrate restoration for sturgeon has been performed in lake sturgeon spawning habitat (e.g., Kerr et al. 2010; Dumont et al. 2011), efforts for white sturgeon are just beginning (Chapter 5; Neufeld and Rust 2007; Crossman and Hildebrand 2012; Chapter 5). While the present results suggest that providing suitable substrate conditions at spawning sites may provide effective restoration of white sturgeon recruitment, it is also important to emphasize the need for field-based verification of the present laboratory experiments to identify suitable longer-term measures for habitat restoration of natural sturgeon spawning sites.

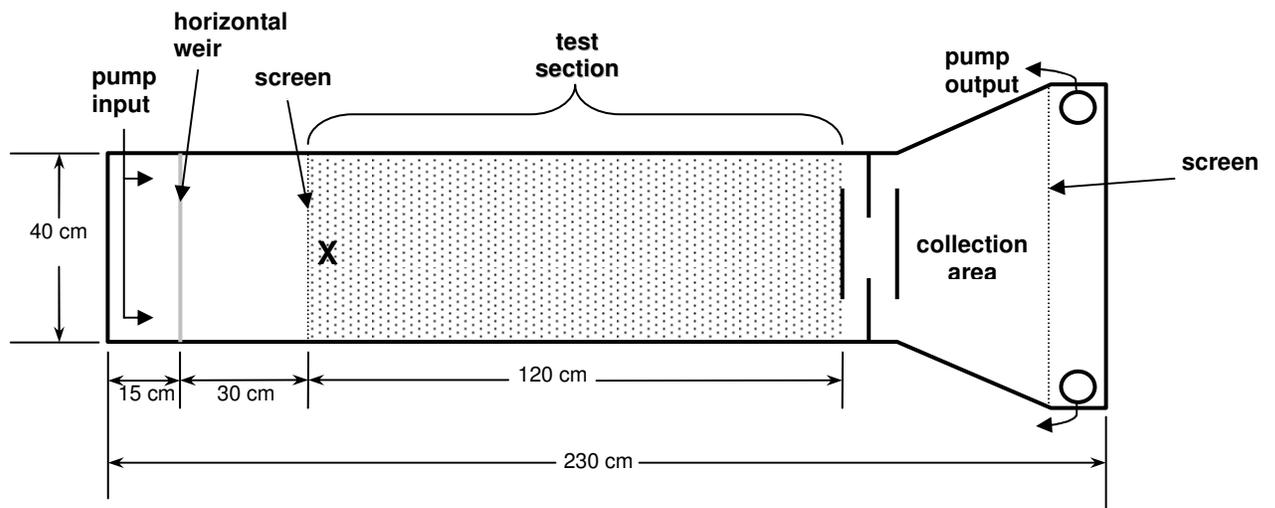


Figure 4.1 Plan view of the Plexiglas flume used for behavioural studies. Water flowed from left to right at a depth of 17 cm. Larvae were released at X. Substrates (described in text) were present only in the test section (stippled area). Previously published in McAdam (2011). © Steven O. McAdam, 2011, by permission.

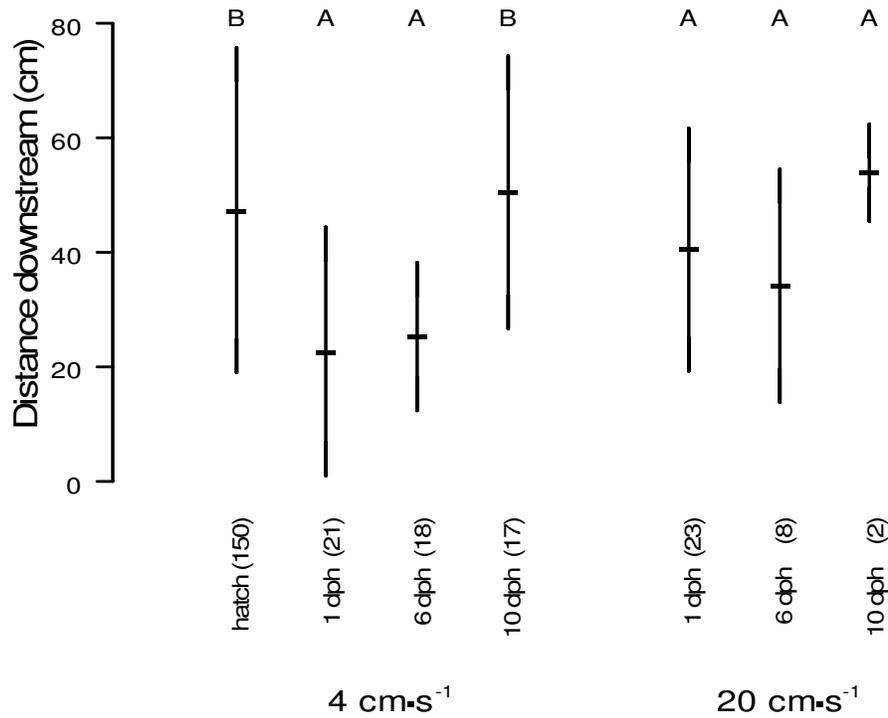


Figure 4.2 Distance downstream from release location for white sturgeon larvae located within small gravel substrate at hatch, 1, 6 and 10 dph (mean \pm SD) and two water velocities. Differences were significant at 4 cm·s⁻¹ (ANOVA, $p < 0.001$) and differences between ages (Tukey test, $p < 0.05$) are indicated by letter codes. The number of hiding larvae in each group is in parentheses. The number of replicate treatments was eight at hatch, six, seven and six for the 1, 6, and 10 dph treatments at 4 cm·s⁻¹, respectively, and six, three, and two for the 1, 6 and 10 dph treatments at 20 cm·s⁻¹ treatments, respectively. Previously published in McAdam (2011). © Steven O. McAdam, 2011, by permission.

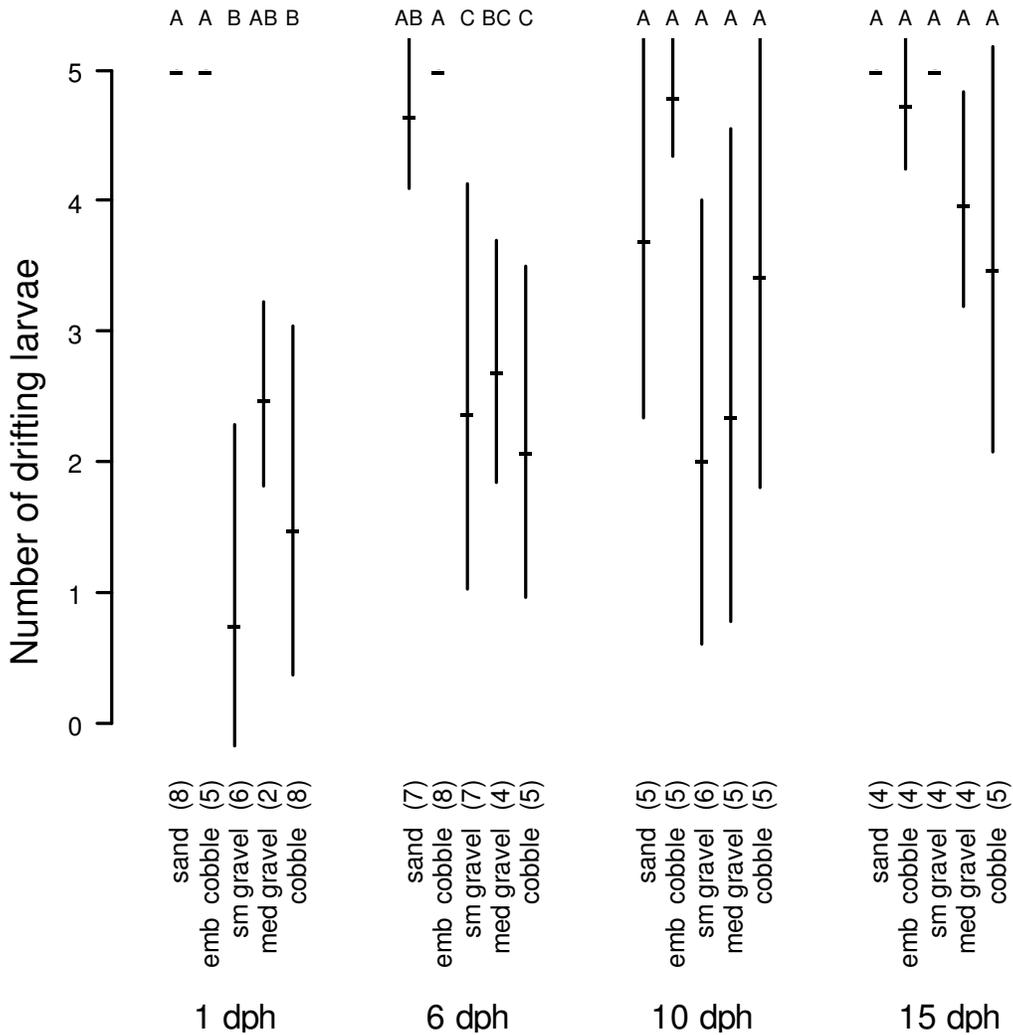


Figure 4.3 Mean number (\pm SD) of larvae drifting at 1, 6, 10 and 15 dph when exposed to various substrates at $4 \text{ cm}\cdot\text{s}^{-1}$ for 10 minutes. Substrate included sand, embedded cobble (emb cobble), small gravel (sm gravel), medium gravel (med gravel) and cobble (grain sizes are identified in the text). Statistically significant differences (ANOVA $p < 0.05$) occurred at 1 and 6 dph, and letter codes indicate differences between treatments (Tukey test, $p < 0.05$). Number of replicates is indicated in parentheses for each age/substrate combination. Previously published in McAdam (2011). © Steven O. McAdam, 2011, by permission.

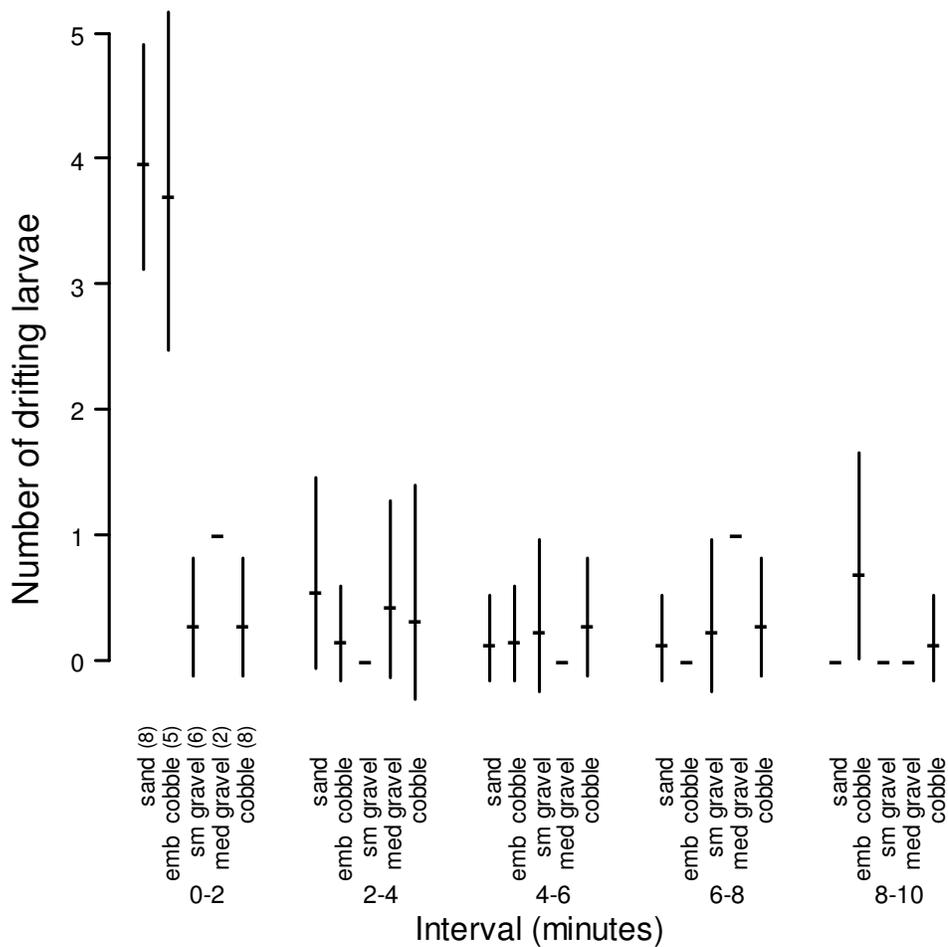


Figure 4.4 Drift of 1 dph larvae at 2 minute intervals (mean \pm SD) in response to sand, embedded cobble (emb cobble), small gravel (sm gravel), medium gravel (med gravel) and cobble (grain sizes are identified in the text). Number of replicates is the same for all intervals and is indicated in parentheses for the 0-2 minute interval. Previously published in McAdam (2011). © Steven O. McAdam, 2011, by permission.

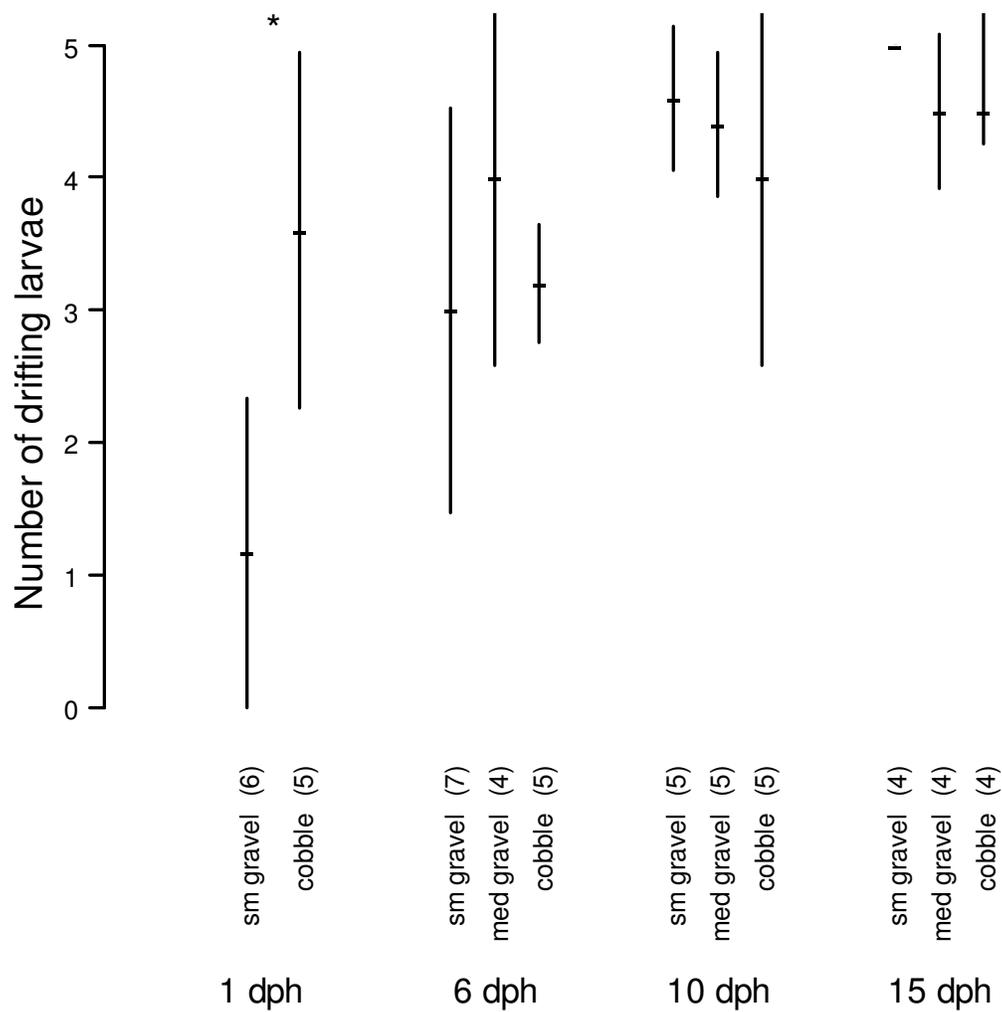


Figure 4.5 Mean number (\pm SD) of larvae drifting at 1,6, 10 and 15 dph when exposed to small gravel (sm gravel), medium gravel (med gravel) and cobble (grain sizes are identified in the text) at 20 cm/sec for 10 minutes. Number of replicates is indicated in parentheses for each age/substrate combination. * indicates statistical significance (t-test, $p < 0.01$). Previously published in McAdam (2011). © Steven O. McAdam, 2011, by permission.

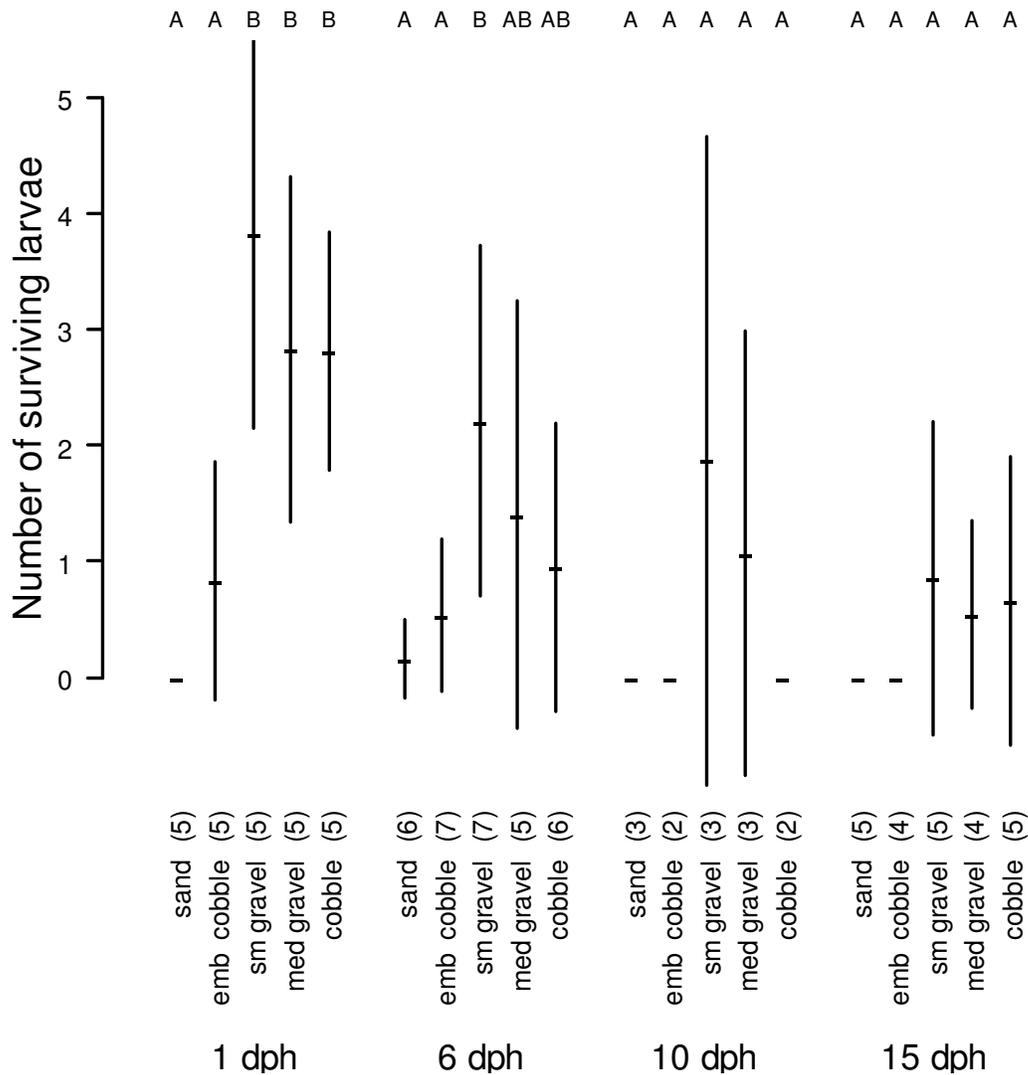


Figure 4.6 Number of white sturgeon larvae aged 1, 6, 10, and 15 dph surviving (mean \pm SD) when exposed to predators over sand, embedded cobble (emb cobble), small gravel (sm gravel), medium gravel (med gravel) and cobble substrate (grain sizes are identified in the text). Statistically significant differences (ANOVA, $p < 0.05$) were observed at 1 dph, and differences between treatments (Tukey test, $p < 0.05$) were identified differences at both 1 and 6 dph (indicated by letter codes). The number of replicates is indicated in parentheses for each age/substrate combination. Previously published in McAdam (2011). © Steven O. McAdam, 2011, by permission.

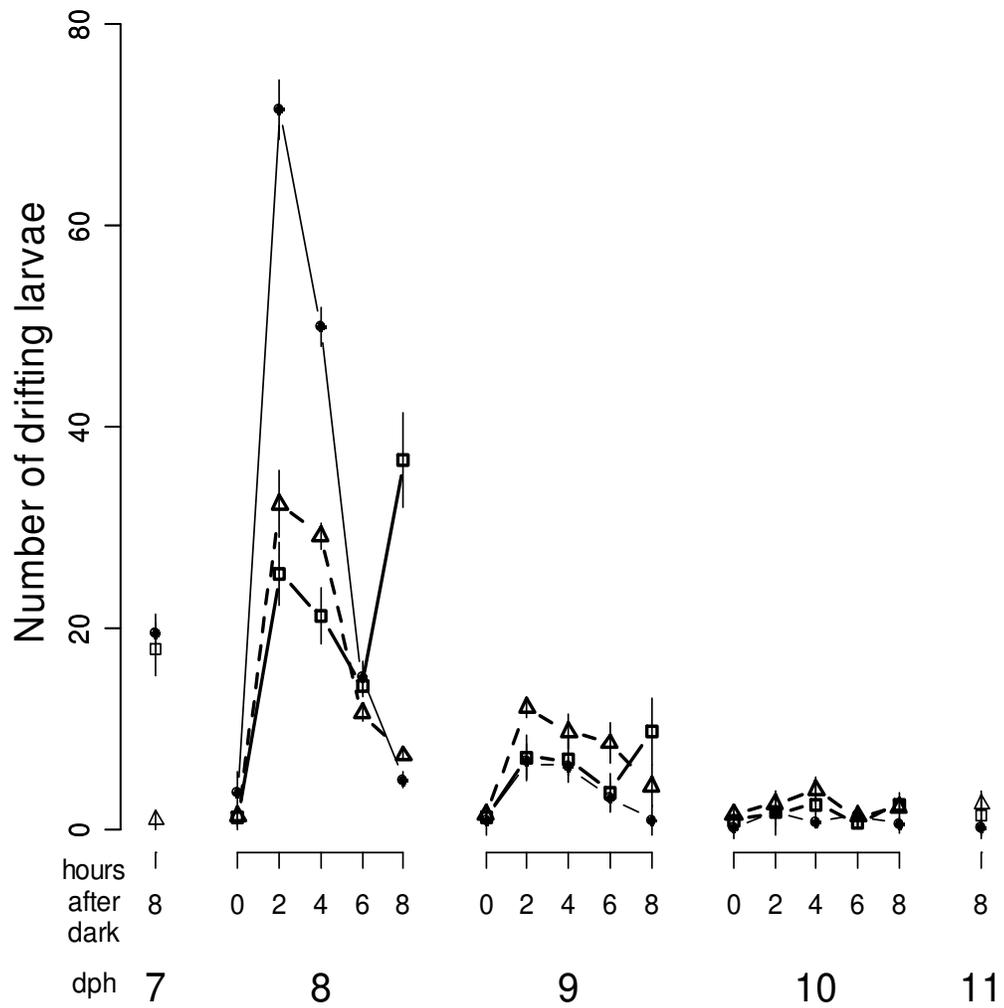


Figure 4.7 The effect of gravel depth on the timing and magnitude of white sturgeon larval drift between 7 and 11 days post hatch. Values represent the mean (\pm SD) of 4 replicate treatments. Gravel depths tested were 2 cm (closed circle), 6 cm (square) and 10 cm (triangle).

Chapter 5 In situ examination of the effects of substrate on behaviour and survival of white sturgeon larvae

Introduction

Yolk sac larvae represent a critical but poorly understood phase in sturgeon life history, and the ecology and habitat use during this period, particularly the decision to remain near the point of hatch versus drift downstream, may have important ramifications for individual survival and population recruitment. The role of substrate in mediating this behaviour and the fate of individuals that remain or drift are key issues that require resolution. Based on the retrospective analysis of recruitment collapse in both the Nechako (Chapter 2) and upper Columbia (Chapter 3) rivers, increased fine substrates at white sturgeon spawning sites were identified as the most likely mechanism of recruitment failure. The laboratory investigations in Chapter 3 identified the biological details of this potential mechanism and showed that interstitial spaces provide hiding habitat for newly-hatched larvae, which diminished downstream drift and increased survival (Chapter 3). Combined with the previous evidence for increased embryo mortality due to smothering by sand (Koch et al. 2006), my findings suggest that early life stages that use interstitial habitats at spawning sites may be primarily affected by changes to riverine substrate conditions. However, continued uncertainty regarding early life history behaviour, particularly under more complex natural conditions, continues to limit a more detailed understanding of the interaction between physical habitat conditions (substrate), early life history biology and recruitment. The recent identification of the importance of substrate condition during early life history for other sturgeon (e.g., Chinese sturgeon – Du et al. (2011); Atlantic sturgeon – Gessner et al. (2009); white sturgeon– McDonald et al. (2009)), combined with the fact that increased fine substrates (i.e. < 2 mm) within river bed gravels are a common result of diminished flushing flows in regulated rivers (Reiser et al. 1990; Ligon 1995) suggests that the effects of substrate condition on

early ontogeny may be a common phenomenon for a variety of sturgeon (Ruban 2005; Nichols et al. 2003).

Although the effects of fine substrate intrusion into the spawning redds of salmon are well studied (Jensen et al. 2009), the large river habitats of sturgeon may explain why similar impacts have not been widely identified. The recent identification of substrate effects on larval growth, development and physiology (Gessner et al. 2009; Zubair et al. 2011; Boucher 2012) also indicates the presence of substrate-mediated effects beyond direct impacts on hiding and survival, which further emphasizes the importance of substrate conditions during early life history. Currently, most studies of substrate-mediated effects on sturgeon have been laboratory based, and although laboratory studies provide greater control over experimental conditions, they cannot fully replicate natural conditions. Intermediate-scale field studies therefore represent a logical progression toward larger-scale habitat restoration. However, *in situ* larval investigations also present challenges due to both the small size of larvae relative to the scale of the river habitats they occupy and the difficulty of experimental manipulation and replication of large-scale environments (e.g., large rivers, marine).

Similar to the suggestion that changes to substrate condition at spawning sites may lead to recruitment failure (Chapters 2, 3 and 4), increased recruitment has been detected in response to restoration of lake sturgeon spawning sites (see Kerr et al. 2010), though not in all cases (Dumont et al. 2011). However, similar experiments for white sturgeon are limited. The experimental release of 1 dph yolk sac larvae has shown increased short-term retention in gravel versus sand substrates (Neufeld and Rust 2008). Longer-term monitoring of restored and unrestored habitat in the Columbia River showed greater retention of released 1 dph larvae in a restored gravel area throughout the yolk sac larvae phase (Crossman and Hildebrand 2012), which agrees with expectations from laboratory results in Chapter 3. By contrast, for pallid sturgeon, Braaten et al. (2008) suggested that drift is the predominant behaviour

of yolk sac larvae; however, their examination of primarily one substrate (sand) and their use of one sampling method (drift sampling) means their results may not represent that species' full behavioural repertoire.

One common feature of spawning habitat restoration studies and larval release experiments is that nearly all studies base their evaluations solely on larvae captured during drift. For example, Braaten et al. (2012) suggest that early larval drift is required despite substantial reductions in the number of larvae captured with increasing distance from the release location. Johnson et al. (2006) is the only study I identified that directly sampled larvae within benthic substrates (though see Forsythe 2010, who conducted *in situ* studies of embryo survival). Additionally, replication and experimental controls were limited in most investigations of sturgeon habitat restoration, with studies either based on uncontrolled before-after comparisons at one site (e.g., Dumont et al. 2011), parallel comparison of one treatment and one control site (Crossman and Hildebrand 2012) or evaluation of a single site with no replication or control (Braaten et al. 2008). While the challenge of replicating large river environments provides an obvious explanation for such limitations, and limited replication does not negate the achieved results, it is important to recognize that standard experimental procedures such as replication can be challenging as the scale of field experiments is increased.

The present study investigated larval responses to more realistic environmental conditions (e.g., substrate, water velocity, presence of predator and food) relative to prior laboratory studies (e.g., Chapter 4; Bennett et al. 2007; Gessner et al. 2009). My study was conducted based on releases of 1 dph yolk sac larvae in side channel enclosures in the Nechako River, which represent field conditions near natural spawning sites. The specific study objectives included the evaluation of behavioural responses (drift versus hiding) to different substrate conditions and the consequences of substrate condition for larval growth and survival. I also examined the effects of releasing larvae upstream of

restored gravel substrates in order to test whether a short period of drift prior to hiding affected survival relative to immediate hiding. Sampling over the full duration of the yolk sac larval phase allowed me to evaluate whether yolk sac larvae show sustained hiding (Gessner et al. 2009) rather than sustained drift, as suggested for some sturgeon (Kynard et al. 2002 a, b). Furthermore, in addition to the central experiment, which examined representative riverine substrates, I conducted smaller-scale tests of the effect of sand substrates for comparison with laboratory findings in Chapter 4. In order to assist interpretation of unexpected results from field experiments, I also conducted an additional experiment to examine how drift net efficiency was affected by set time and net configuration.

Methods

Field study of substrate effects on larval drift, retention, growth and survival

To determine how substrate affects drift, I evaluated different substrate treatments within individual replicate side-channel habitats located on the floodplain of the Nechako River. Treatments included three different substrate types (embedded natural substrate, sand and added un-embedded gravel). Additionally, larvae were released both directly onto added gravel or 40 m upstream of the augmented gravel area (forcing larvae to drift over unsuitable substrate before encountering a suitable patch for settling). Two replicates of each treatment were conducted.

White sturgeon larvae were obtained from spawning of broodstock captured from the Nechako River. Five male and five female white sturgeon (leading to 10 unique crosses) were spawned in Prince George, BC following induction by hormone injections. Eggs were fertilized, treated with a mud solution according to Conte et al. (1988) to deactivate their adhesive layer, and then transported to a streamside rearing facility in Vanderhoof, BC. Eggs were maintained in upwelling incubators (McDonald jars) using filtered river water maintained at 15°C. At 1 day post hatch (1 dph), larvae from distinct crosses (at a minimum females were distinct) were released at ten sites in the Nechako River (Figure

5.1; distinct crosses were utilized to allow future identification of treatments if recruitment was detected). The number of larvae released into each field site (rounded to the nearest 100) was determined by batch wet weights divided by the wet weight of a counted subsample, or, for sand treatments, by direct counting.

Larvae from all crosses were also retained at the hatchery and reared at 15°C. For hatchery-reared larvae, feeding began at 10 dph and larvae were fed to satiation six times per day using a mixture of equal parts EWOS zero fish food (EWOS Canada Ltd.), powdered krill and Cyclop-eeze (Argent Chemical Laboratories). Eight larvae were sampled every second or third day for comparison with river-reared larvae.

Larval release sites were located in the spawning reach of the Nechako River near Vanderhoof, BC (Figure 5.1). Water level and temperature data were obtained from the Water Survey of Canada gauge (08JC001) at the downstream end of the study reach. Side channel locations were selected based on the need for independent locations (i.e., no potential for larval drift between sites) and accessibility by wading. Within those constraints, sites were selected based on substrate conditions and to maximize depth and velocity (in order to make them representative of mainstem conditions and because the experiment was conducted during a period of declining water levels). Substrate treatments were conducted within a 10 m long study site with substrate consisting of unperturbed embedded gravel/cobble (sites N1 and N2), a 10 m long section of introduced clean gravel (grain size = 12 mm-36 mm) (sites G1 and G2), or within a larger study site (sites 40m1 and 40m2) that combined 40 m of unperturbed substrate (similar to sites N1 and N2) upstream of a 10 m introduced clean gravel (similar to sites G1 and G2). All treatment areas were enclosed on both sides by barrier nets (1 mm fiberglass screen) in order to standardize edge conditions and eliminate lateral larval drift that might confound treatment effects. For sites 40m1 and 40m2, barrier nets were connected to the banks of the

side channel at the upstream end of the 10 m augmented gravel area; vegetation in the upper 40 m was removed to limit possible riparian effects. Site width varied from 3.8 m to 8.1 m (Table 5.1).

Washed natural river gravel was delivered to the river bank adjacent to study sites by helicopter. Gravel augmentation was conducted using hand shovels to place gravel over existing embedded gravel substrate to an average depth of 6 cm (range 4 cm to 8 cm). Gravel placement occurred from two to five days prior to release of 1 dph larvae.

Treatments (natural, gravel, combined) were replicated once each during two temporal rounds (experimental blocks) of the experiment, which began on May 30 and June 11, 2008, respectively. Roughly equal numbers of larvae were released at eight locations (two rows of four) at the upstream end of each site. In round 1, larvae were released near the substrate by placing inverted buckets on the river bottom, then removing the bucket from the lid after a two-minute acclimation period. Because the presence of buckets and proximity of the release technician created turbulence that caused larvae to enter the water column, for round 2 larvae were released directly above the substrate through a 7.5 cm diameter pipe oriented upstream about 1 m to the side of the release technician.

Larval drift was monitored using a single drift net located near mid-channel at the downstream end of each site. Drift nets were attached to steel posts driven into the river bottom, and sampled the entire depth of the water column. Net opening dimensions varied with water depth, and width was maximized for any given depth (net circumference = 3.3 m). Rectangular net openings were used in round 1. Due to concerns that high suspended sediment loads and extended set durations reduced sampling effectiveness, net openings used in round 2 were right angle triangles (narrow near surface) that sampled roughly half the area of the round 1 net configuration. Drift nets were sampled at 30 minute intervals for the first two hours, at eight hour intervals for the first two days, and then at 8 hour intervals every second day. In round 2 daily sampling was reinstated at 12 dph once feeding larvae

were detected; however, due to greater sampling intensity midday samples were not taken at either 13 or 14 dph for all round 2 sites or at 15 dph for site N2. Sampling was also limited for site G2 at 17 dph due to equipment theft.

Because initial study goals included creating an effect size capable of leading to detectable recruitment, destructive benthic sampling was not initially planned. However, benthic sampling was implemented part way through the study due to the failure to detect larval drift at the expected time in round 1. The presence of larvae in benthic habitat was determined by benthic sampling roughly every second day beginning June 16, 2008 (20 and seven days after the initiation of rounds 1 and 2, respectively). The delayed initiation of benthic sampling was in response to the lack of drifting larvae detected during round 1. Sampling initially examined a 32 cm X 30 cm area using a Surber sampler; however, due to low densities at most sites a larger 74 cm x 74 cm area was sampled from June 18 onward. For augmented gravel sites a hand trowel was used to disturb substrates within the sample area (i.e., to disturb the full depth of the augmented gravel). As substrates at control sites were embedded, a rake was used to disturb the substrate surface and stimulate larval drift into the Surber sampler at those locations. Density estimates were scaled up to provide an abundance estimate for the whole treatment area, and survival rates were calculated relative to the estimates of larvae remaining at 2 dph (Table 5.1). Typically, two samples were taken at each sampling period for a total sampled area of 1.1 m², which represented 1.4% to 2.9% of the total site area. Site N1 was not sampled after 25 dph, at which time 5.48 m² of the site (6.7% of total site area) was sampled, and the failure to detect larvae was considered confirmation of their absence. Sampling at site 40m² was also limited from 18 dph to 23 dph as the theft of my boat prevented access during that period. Sample locations within sites were located randomly in locations that could be accessed with minimal site disturbance and without affecting drift net sampling. Sample sites were also marked to avoid duplicate sampling.

Sand substrates were not common in the spawning reach of the Nechako River, and the sand treatment was conducted principally for comparison with prior laboratory findings. Sand sites measured 1 m x 10 m (W x L) and were enclosed on either side with 1 mm screen. Water levels during round 1 limited the availability of a suitable test site. As a result, only one sand treatment was conducted during round 2 (S2). Data are also presented for a second sand site (S3) where a previous pilot test was conducted in July 2005 (larval procurement methods were the same in 2005 as in 2008). A total of 100 larvae were released for the S3 test, and 1,500 were released at S2. The lower release numbers for site S3 occurred because it was a pilot test. Larvae were released at site S3 using an inverted 500 mL container placed on the substrate, and larvae were released after a two minute acclimation period by lifting the container off its lid. Larvae were released at S2 in the same manner as other round 2 sites. Due to the restricted width of these sites, the downstream drift nets covered the whole channel area and samples represent the total drift for each interval. Sand sites were also only monitored during the two-hour initial drift phase.

Samples collected from drift net cod ends were transferred to buckets and cod ends were rinsed at least twice into the collection bucket. Drift nets were thoroughly rinsed once to ensure all captured larvae were sampled. Larvae were counted by sequentially placing small volumes of the sample into a flat opaque counting tray, diluting with clean water and carefully looking for larvae. Sub-sampling was done only for samples that included large amounts of detritus (in round 2 between 2 and 10 dph). Sub-sampling consisted of splitting samples evenly and then one sample was randomly chosen for evaluation. In June 2009 five samples with no larvae were seeded with five larvae each to evaluate sampling accuracy.

All sampled larvae were preserved in 10% formalin, and weight and length were measured within three to four months after capture using formalin-preserved samples. Weight was measured to +/- 0.1

mg, and length was measured using digital calipers under a compound microscope. Due to limited sample sizes, at most times and for most treatments larval weights were only statistically compared for site G2 versus site N2 at 11 dph and site G2 (benthic and drift samples) versus the same family maintained in the hatchery. The first comparison was based on a t- test, and the second used ANOVA followed by individual comparisons using Tukey tests according to Zar (1984).

Evaluation of net efficiency

In order to determine whether decreased drift net efficiency affected larval captures during round 1 of the experiment, I evaluated the effect of net soak time and drift net configuration on capture efficiency in June and July 2009. Larvae were again obtained from captive spawning of Nechako River white sturgeon (two females and three males), as described above, and tests examined larvae at both 1 dph and 12 dph. Drift net configurations were as described above, with ten nets located at least 1 m apart in two side channels (sites G2 and N1). Triangular or rectangular openings were randomly assigned to individual locations. After leaving nets to soak for periods of 0, 2, 4, 6, 8 and 10 hours (6 and 10 hour treatments were omitted for 12 dph), ten larvae were released 15 cm upstream near the bottom at the midpoint of the net. The net was immediately retrieved and sampled as described above and capture efficiency was evaluated relative to soak time and net configuration. Five replicates were conducted at 1 dph (except n = 4 for 10 hour test) and four replicates were conducted at age 12 dph. Statistical evaluation was based on ANOVA followed by individual comparisons using a Tukey test (Zar 1984).

Results

Field study of substrate effects

Retention of larvae within all treatments was apparent based on the extent of initial drift and the detection of larvae based on benthic sampling. However, survival differences between substrate

treatments indicate strong benefits of interstitial hiding. An initial drift pulse was identified in all treatments (Table 5.1 and 5.2). The estimated proportion of larvae that drifted out of the study site within the first two days after release varied from 0.46 to 0.83 (Table 5.1). However, the short duration of the initial drift pulse is demonstrated by the finding that for all treatments, most of the larvae caught in the first two days were captured within the first 30 minutes (95%, range 92% - 98%). For round 2 sampling, the initial drift pulse included a lower proportion of released larvae for sites 40m2 and N2, but not for G2. If changes to the larval release method affected initial drift, effects were therefore not consistent between sites. Sand substrates led to higher drift within the first two hours (S2 = 93%, S3 = 82%); however, differences in the proportion of larvae in the initial drift pulse were not statistically significantly different for any treatments (ANOVA, arcsine transformation, $p > 0.05$). Limited replication and the release protocol used in round 1 may have limited the ability to identify differences statistically.

Subsequent to the initial drift pulse, few larvae were caught between 2 dph and 10 dph, inclusive (Table 5.2). No drifting larvae were captured after day six in round 1, however, results may be biased by drift net capture efficiency (see below) and erosion of the river bed below the net (particularly at site G1). During round 2 after 10 dph 1, 37, and 0 larvae were caught in drift nets at sites N2, G2 and 40m2, respectively. Based on site G2, the capture of 35 of 37 larvae in the 0800 sample indicates that drift by feeding larvae is primarily nocturnal. For site G2, based on the proportional site width sampled, the estimate of the total number of larvae that survived and drifted was 775, or 6.3% of the larvae estimated to be present at 2 dph. Counts from samples seeded with five larvae identified 5, 5, 5, 4 and 4, indicating a detection probability of 92%. Conceivably, a single larvae might therefore go undetected ($p = 0.08$), but it is unlikely that two or more ($p = 0.0069$) would go undetected.

Because benthic sampling started when round 1 larvae were 18 dph, changes in benthic density are most informative for round 2. Site G2 showed the highest survival through the yolksac larvae

period (Figure 5.3). Survival of 49.6% and 31.5% of larvae at 5 and 7 dph respectively declined to estimated survival of 5.6% and 14.0% of larvae at 11 and 13 dph, respectively. Although drift was detected at this site, densities of larvae subsequent to the drift pulse indicate that 5.0% and 4.1% (mean = 5.6%) of the larvae retained at 2 dph were still present at 15 dph and 17 dph, respectively. While larvae were detected at site 40m2 at 5 dph, estimated survival (Table 5.3, Figure 5.3) was near zero even before detection of drift at site G2, and declined to zero by 11 dph. In contrast to sites with augmented gravel, site N2 showed survival estimates near zero at all times, although three larvae were detected with benthic sampling at 13 dph, and one drifting larvae was caught at 11 dph. Benthic sampling also detected feeding larvae from 16 dph to 27 dph at multiple sites subsequent to the expected timing of drift based on site G2. Feeding larvae within substrates were most consistently detected at site G2, and the infrequent detection of relatively high densities for one sample each from sites G1 ad 40m1 (Table 5.3) suggests a patchy distribution of interstitially-located feeding larvae.

Growth of yolk sac larvae was evident for all treatments, including outplanted river-reared larvae and hatchery-reared larvae. Hatchery rearing showed a general pattern of weight gain until about 7 dph and a plateau until 15 to 20 dph, followed by rapid weight gain thereafter (Table 5.4). Weights were generally stable between 12 and 14 dph, so river-reared fish (benthic and drift) between those ages were pooled for each capture method. Comparison of weight for larvae captured by benthic sampling from sites G2 and N2 at 11 dph indicates that larvae at site G2 weighed significantly more (two-tailed t- test, $p < 0.05$); however, the sample size for site N2 is small. This comparison also does not account for family effects as larvae from different families were released at these two sites. Based on the similarity in their summed daily mean temperature (accumulated thermal units = ATU), comparisons were made with hatchery-reared larvae aged 11 dph and 13 dph (165 to 195 ATU) and river reared larvae aged 12 to 14 dph (167 to 197 ATU) from the same parents. Benthic- (mean \pm SD; 54.5 ± 23.0 mg) and drift- (57.4 ± 6.0 mg) captured larvae at site G2 weighed significantly more than the

same family reared under hatchery conditions ($48 \pm 2.7\text{mg}$) (ANOVA, $p < 0.05$), but were not significantly different from each other.

Over the course of the experimental period water temperature as measured at the WSC gauge at Vanderhoof varied from 12.6°C to 16.4°C and showed a general warming trend (Figure 5.2). Water level measured at the same site declined by 0.92 m. While both water level and temperature varied over the course of both round 1 and 2 of the experiment, changes are not expected to affect results.

Evaluation of net efficiency

The efficiency of larval drift capture declined with set duration due to the clogging of nets with fine debris (Figure 5.4). Rectangular net openings led to significant declines (ANOVA, $p < 0.05$) in capture efficiency with four hour soak times, and were near zero efficiency by six hours at 1 dph and eight hours at 12 dph. In contrast, the efficiency of triangular net openings showed a statistically significant decrease for eight hour soak times (ANOVA, $p < 0.05$), although mean net efficiency was still 27.5%. Observed flow patterns for rectangular net openings indicated that longer set times led to upstream currents along the base of the net, the result of a combination of higher near-surface water velocities and decreased porosity due to accumulation of fine debris. Erosion of the river bed at the base of the nets was also observed and likely decreased net efficiency. Similar effects were not observed for triangular net openings.

Discussion

Detection of larvae after the age of 5 dph (and up to 27 dph) at sites with restored gravel substrates as compared to near zero survival at sites with unperturbed embedded substrate indicates that the presence of interstitial habitat increased survival. The identification of increased survival of larvae placed directly onto the gravel relative to sites where a short drift period was required supports the previous suggestion (Chapters 2, 3 and 4) that immediate hiding in the vicinity of hatch should be

favourable for white sturgeon. The identification of clear survival benefits combined with the detection of increased growth both emphasize the importance of interstitial habitats for yolk sac larvae and support the possibility that decreased quantity and quality of interstitial habitat may contribute to recruitment failure. Finally, the detection of higher initial drift differed from the previous laboratory study (Chapter 4) emphasizes that releasing larvae into the water column does not emulate the natural hatch location of larvae. As a result, release protocols that do not account for this limitation may bias our understanding of this life stage.

While field studies can provide important validation of both laboratory findings and retrospective evaluations of the potential causes of recruitment failure, implementing experimental studies within the Nechako River during the freshet period was challenging. In particular, the effects of high levels of waterborne debris and organic matter led to unanticipated declines in the effectiveness of drift sampling in round 1 of this study; however, these limitations were resolved in round 2. While the inclusion of benthic sampling was not initially planned (in order to maximize the number of surviving larvae and the possibility of detecting future recruitment), the late addition of this sampling method was fortuitous and provided results that were complementary to information derived from drift sampling.

Similar to other larval release studies of white sturgeon (Neufeld and Rust 2008; Crossman and Hildebrand 2012), an initial drift pulse occurred in all treatments. The magnitude of the initial drift pulse was higher than expected based on the laboratory study in Chapter 4, which showed that a majority of larvae hid within four to 13 seconds in the presence of suitable substrate. The observed difference in the present field experiment likely reflects a combined effect of larval release methods, higher water velocity and the short length of test sites. While I released yolk sac larvae near the substrate, the turbulence at the point of release caused larvae to move into the water column.

Coupled with the short length of experimental sites, this release method would have biased initial drift upwards relative to a natural situation where larvae hatch interstitially. Larvae might also experience some degree of disorientation upon release, which would also increase drift estimates.

Although immediate hiding by the majority of larvae was not apparent in the present results, Crossman and Hildebrand (2012) detected a relatively small initial drift pulse by yolk sac larvae in their investigation of Columbia River white sturgeon. In that study the absence of high initial drift in response to restored substrates likely resulted from their longer test area (100 m) and the release of larvae during a period of zero flow from the upstream Revelstoke Dam. The detection of little or no drift by lake sturgeon yolk sac larvae immediately after hatch (Auer and Baker 2002), and only in the immediate vicinity of spawning sites (Kempinger 1988), also suggests a rapid transition to interstitial hiding for that species, which is similar to the behaviour of white sturgeon observed in Chapter 4. The higher mortality of lake sturgeon eggs located on substrate surfaces due to predation (Johnson et al. 2006; Forsythe 2010) indicates that surviving embryos would primarily be located in substrate interstices, and as a result most eggs would naturally hatch within the substrate matrix. Therefore, releasing larvae anywhere in the water column creates an unnatural experimental starting point. While *in situ* studies may provide important verification of laboratory studies, the present findings also indicate the continued potential for bias due to larval release methods. Such limitations may be critical to the interpretation of results when an initial drift pulse is detected.

Variation in water temperature should not have substantially affected present results (e.g., due to effects on developmental rate) because mean temperatures showed relatively little variation. During round 1 in particular they were similar to the 15°C rearing temperature in the hatchery. While decreasing water level over the course of the experiment created logistical challenges (e.g., with respect to identifying suitable experimental sites), conditions within all sites remained representative of

initial conditions, and variation from this source should not have affected my findings to any significant degree. The primary difficulty caused by riverine environmental conditions was the high suspended debris loads during the freshet period and the resultant effects on drift sampling effectiveness. Observation of water under-cutting drift nets limited sampling effectiveness to an unknown extent (particularly at site G1). Additionally, evaluation of net efficiency changes over the eight hour sampling interval showed that the net configuration used in round 1 of this study led to decreased efficiency after four hours and nearly zero efficiency by six hours. These findings suggest that after 1 dph, when sampling shifted to an eight hour sampling interval, drift results from round 1 may not accurately reflect actual drift. Fortunately, similar problems were not encountered with the net configurations used in round 2.

Despite limitations caused by low capture efficiency larvae were detected at both sites with augmented gravel during round 1 (40m1 and G1) based on either drift or benthic sampling, but no larvae were detected by either method at site N1 after 3 dph. Similar results were also achieved during round 2. The detection of a clear drift pulse between 12 dph and 14 dph at one site (G2) combined with the lack of drift from 3 dph to 12 dph indicates that hiding by yolk sac larvae is continuous once initiated. Sustained hiding by yolk sac larvae was also observed in the laboratory evaluation of the effects of gravel depth (Chapter 4). This observation contrasts with the prior suggestion of slow downstream drift by white sturgeon yolk sac larvae (Kynard and Parker 2005, 2010), but agrees with patterns for lake sturgeon (e.g., Auer and Baker 2002; Kempinger 1988) and Atlantic sturgeon (Gessner et al. 2009). Both field and laboratory components of the present study also show that drift by feeding larvae is nocturnal, which has also been demonstrated for lake sturgeon (e.g., Auer and Baker 2002). The congruence between studies of white sturgeon (present study; Crossman and Hildebrand 2012), lake sturgeon (Auer and Baker 2002) and Atlantic sturgeon (Gessner et al. 2009) suggests white sturgeon as well as other sturgeon species may show a two-stage pattern that includes continued

hiding after hatch (i.e., they do not emerge and drift) followed by drift at the initiation of exogenous feeding.

Although the magnitude of the initial drift pulse is similar for all treatments, this also suggests that larvae were initially retained within treatment areas. Relative to the low levels of retention for embedded substrates in Chapter 4, higher larval retention in conjunction with naturally-embedded substrates may reflect the greater roughness of natural substrates relative to those in laboratory experiments (Chapter 4). However, while hiding behaviour leads to retention in such areas (present study; Crossman and Hildebrand 2012), low subsequent densities indicate nearly 100% mortality associated with substrates that prevent interstitial hiding. In contrast, because survival was apparent at all sites with augmented gravel, there is likely a real survival advantage provided by interstitial habitat (Gotceitas and Brown 1993; Johnson et al. 2006; Jennings et al. 2009). Fish predation is the assumed source of mortality (not quantified in my study) and, relative to short-term tests in Chapter 4, the survival of larvae in conjunction with augmented substrates demonstrates the long-term survival benefits of interstitial habitat. Additionally, decreased larval densities prior to the detection of drift suggests a period of increased vulnerability to predation immediately prior to drift (Figure 5.3), possibly due to increased larval movement prior to emergence (personal observation). Considering both drifting and retained feeding larvae for site G2 suggests an overall survival of 10.9% relative to the estimated number of larvae at 2 dph, which is slightly lower than the 16% estimate for lake sturgeon (Johnson et al. 2006). In combination with decreased survival of eggs located on the surface of benthic substrates (Johnson et al. 2006; Forsythe 2010), the present identification of zero survival for yolk sac larvae in the absence of interstitial hiding habitat provides further evidence that increases in fine substrates and the infilling of interstitial habitats provide a mechanism which would contribute to recruitment failure at the whole river scale.

Similar to the identification of a “drift” versus “hiding” dichotomy in laboratory studies (Chapter 4), recent field studies show a similar split between studies that emphasize drift (Braaten et al. 2008, 2012) and those that emphasize hiding (present study, Crossman and Hildebrand 2012). However, both behaviours may play important roles. Interstitial hiding in the vicinity of spawning habitat should be the predominant behaviour when substrates are suitable (Gessner et al. 2009; Chapter 4); however, drift by yolk sac larvae may increase survival relative to areas where larvae are unable to access interstitial habitat. While larvae were retained in unaltered sites (N1 and N2; Crossman and Hildebrand 2012), subsequent survival was near zero. Presumably this result reflects a substrate condition that provides hydraulic refuge suitable for larval retention, but that is insufficient to provide cover from predators. In contrast, the detection of larvae within the 40m² treatment area at 5 and 7 dph demonstrates that short-term drift followed by hiding in suitable habitat allowed some larval survival, although survival was demonstrably lower than for immediate hiding (site G2). This finding emphasizes the importance of considering both drift and hiding behaviour, and in particular how they affect survival. Both behaviours may be adaptive, but in different contexts.

The present investigation examined multiple substrate treatments and monitored both drift and hiding behaviour throughout the yolk sac larval phase, which is unique relative to prior studies, which predominantly measure drift responses to one or two substrate conditions. Despite the importance of interstitial hiding, this is only the second study (see Johnson et al. 2006) to specifically investigate yolk sac larvae within benthic habitats. Survival through the yolk sac larvae phase when larvae were released directly over (e.g., site G2) or upstream (e.g., 40m²) of augmented gravel substrate suggests that sustained hiding or larval emergence and drift comprise distinct behavioural tactics, with the latter being a secondary tactic used by larvae that cannot access interstitial hiding habitat. Identification of immediate hiding as the preferred tactic is also supported by retrospective evaluations. While drift by pallid sturgeon yolk sac larvae has been suggested (Kynard et al. 2007; Braaten et al. 2008, 2012),

analysis based on fin ray chemistry (Phelps et al. 2012) shows that of the pallid sturgeon larvae that survive, most do not undergo long-range drift. The absence of long-range drift is also suggested by the presence of localized recruitment dynamics, which are particularly evident for the WAN stock in the Columbia River (Chapter 3).

Interstitial rearing also leads to more rapid growth (Boucher 2012), which likely confers a further survival benefit as larval predation risk decreases with prey size (Werner and Gilliam 1984; Anderson 1988; Fuiman 1994). Both the present results and Crossman and Hildebrand (2012) have detected significant growth differences under field conditions. Similar effects of early life history exposure to substrate have also been observed for species, including various salmonids (e.g., Peterson and Martin-Robichaud 1995; Kihlslinger and Nevitt 2006) and robust redhorse (Jennings et al. 2010). While the direct survival consequences of poor substrate condition may be sufficient to explain recruitment failure, the variety of recent studies that identify the importance of substrate to physiological condition and growth of sturgeon (Gessner et al. 2009; Boucher 2012; Zubair et al. 2012) also emphasize that more subtle and indirect effects will also affect survival, and may contribute to recruitment variation under more natural conditions.

Drift by early feeding larvae is widely observed (e.g., Chapter 4; Kempinger 1988; Auer and Baker 2002; Howell and McLellan 2007), and therefore the retention of feeding larvae within augmented substrates after the detection of a drift pulse was unexpected. However, while the ontogenetic transition from yolk sac larvae to feeding larvae is associated with both the initiation of feeding and drift, the timing of these events is not necessarily synchronous (Urho 2002). While the timing of larval drift may be influenced by the need to encounter food, larvae may be able to encounter food within interstitial habitats (e.g., benthic invertebrates) without resorting to drift and its associated risks. Although such a strategy would be beneficial if it increased survival, the decreased weight of both

drifting and benthic larvae captured after 15 dph, relative to those from 12 to 15 dph, suggests survival benefits may be of short duration. An alternate explanation is that larvae were trapped within the substrate matrix, and the negative effect of gravel depth on the number of drifting larvae (Chapter 4) suggests larval entrapment provides a more likely explanation for the extended interstitial presence of feeding larvae beyond 15 dph.

Recruitment declines for at least three sturgeon species have now been linked to substrate change (white sturgeon – Chapter 2,3 ; Paragamian et al. 2009; lake sturgeon – Nichols et al. 2004; Chinese sturgeon – Du et al. 2011), and the higher survival of interstitial eggs (Johnson et al. 2006; Forsythe 2010) and yolk sac larvae (Chapter 4; Gadomski and Parsley 2005) when interstitial habitats are available indicates a direct mechanism by which substrate changes could lead to recruitment failure. Additionally, the effects of substrate condition on sturgeon growth (Gessner et al. 2009; Boucher 2012) and stress responses (cortisol levels; Zubair et al. 2011) identify important secondary effects that may also limit survival. In contrast to the focus on drift for other sturgeon (e.g., Kynard et al. 2007; Braaten et al. 2012), the combination of survival and the growth benefits of substrate condition during early life history emphasize that a more thorough understanding of early larval behaviour and survival will benefit both our understanding of recruitment failure and the effectiveness of restoration. While most studies of sturgeon yolk sac larvae have been conducted under controlled laboratory conditions, medium-scale field tests such as the present study provide an important step in the incremental progression toward large-scale restoration. While larger-scale projects will be required to provide more permanent habitat restoration, recent examples of lake sturgeon spawning habitat restoration (Kerr et al. 2010; Dumont et al. 2011) suggest that similar approaches should be suitable for white sturgeon.

Table 5.1 Descriptive data regarding conditions at the drift net location, the proportion of larvae sampled in the first two days and the estimated number remaining at 2 days post hatch. Both depth and velocity were measured at nine locations for each site except sand sites and were based on three measurements. For round 2, net widths are the mean submerged width due to the triangular net configuration.

Site	Depth (cm) (range)	Velocity (m/sec) (range)	Site Width (net width)	Total released	Estimate of proportion sampled in first 2 days	Estimated number remaining at 2 dph
G-1	55(46-61)	0.62 (0.46-0.76)	4.25 (0.50)	42900	0.59	17439
G-2	50 (35-63)	0.46 (0.35-0.60)	5.45(0.26)	29600	0.59	12232
40m-1	55 (43-61)	0.56 (0.41-0.62)	3.8 (0.47)	28600	0.83	4948
40m-2	69 (58-76)	0.60 (0.46-0.71)	6 (0.27)	40300	0.48	20849
N-1	67 (48-83)	0.56 (0.41-0.64)	8.1 (0.70)	19800	0.62	6809
N-2	62 (51-71)	0.35 (0.30-0.39)	6.3 (0.35)	21900	0.46	11737
S-2	55 (52-58)	0.58	1.0 (1.0)	1500	-	--
S-3	45 (43-48)	0.61	1.0 (1.0)	50	-	--

Table 5.2 Number of drifting larvae caught shortly after release and over first 19 days of the larval period. Samples for 1 dph indicate larval captures at 22:00 on day 0 and 06:00 on day 1. Later samples indicate midday (14:00), dusk (22:00) and overnight (06:00) samples, respectively. Dashes indicate missed samples (see methods). In all cases, a single net was used with either a rectangular (sites G1, N1, 40m1, S2, S3) or triangular (sites G2, N2, 40m2) opening.

Time (min) or Age (dph)	Site							
	G1	G2	N1	N2	40m1	40m2	S2	S3
30 (min.)	2922	1212	1055	771	2832	1271	1373	38
60 (min.)	43	4	62	48	35	22	16	1
90 (min.)	4	2	0	11	15	2	8	1
120 (min.)	4	1	2	4	9	0	3	1
1	11, 17	5, 0	0, 0	5, 0	23, 7	- , 2		
2 - 3	5, 1, 5	2, 2, 0	0, 0, 1	0	2, 0, 1	0, 0, 0		
4 - 5	0, 0, 1		0, 0, 0	0, 0, 0	0, 0, 3	0, 0, 0		
6 - 7	1, 0, 0	0, 0, 0	0, 0, 0		0, 0, 0	0, 0, -		
8 - 9	0, 0, 0	0, 0, 0	0, 0, 0	0, 0 -	0, 0, 0	0, 0, -		
10 - 11	0, 0, 0		0, 0, 0	0, 0, -	1, 0, 1			
11 - 12		- , - , 8		- , - , 0		- , - , 0		
12 - 13	0, 0, 0	0, 1, 17	0, 0, 0	0, 0, 0	0, 0, 1	0, 0, 0		
13 - 14		- , 0, 6		- , 0, 0		- , 0, 0		
14 - 15	0, 0, 0	- , 0, 3	0, 0, 0	- , 1, 0	0, 0, 0	- , 0, 0		
15 - 16		0, 1, -		- , 0, 0		0, - , -		
16 - 17	0, 0, 0	0, 0, 1	0, 0, 0		0, 0, 0			
17 - 18		- , - , 0		0, 0, 0		0, 0, 0		
18 - 19	0, 0, 0	0, 0, 0	0, 0, 0	0, 0, 0	0, 0, 0	0, 0, 0		

Table 5.3 Benthic sampling details for the benthic capture of larvae. Details for each sampling date include the number of replicate samples followed by the catch for each sample, and finally the total area sampled in m² in parentheses. In cases where replicate samples were pooled in the field, only the total number of sampled larvae is recorded (e.g. 21 larvae for site G2 at 4 dph).

Dph	G1	G2	N1	N2	40m1	40m2
4		2 – 21 (0.19)				
5						3 – 5, 4, 0 (0.29)
7		1 – 14 (0.096)		4 – 0, 0, 0, 0 (0.38)		2 – 3, 0 (0.20)
9				2 – 0, 0 (1.10)		
11		1 – 7 (0.55)				2 – 0, 0 (0.20)
13		1 – 15 (0.55)		3 – 3 (1.65)		2 – 0, 0 (1.10)
15		2 – 0, 9 (1.10)		3 – 0, 0, 0 (1.65)		
16						2 – 0, 0 (1.10)
17		2 – 1, 10 (1.10)				
18	2 – 0, 0 (0.19)		2 – 0, 0 (1.50)	3 – 0, 0, 0 (1.65)	1 – 9 (0.76)	
19		2 – 6, 10 (1.10)				
20					2 – 0, 0 (0.19)	
21	1 – 6 (0.54)		2 – 0, 0 (1.10)		2 – 14 (1.10)	
23		1 – 19 (0.55)				2 – 3, 0 (1.10)
25	2 – 0, 3 (1.10)		10 – 0 (5.48)		2 – 1, 1 (1.10)	2 – 0, 0 (1.10)
27		1 – 2 (0.55)				2 – 0, 0 (1.10)
29					2 – 0, 0 (1.10)	
30	B – 0, 0 (1.10)					

Table 5.4 Mean weight (\pm SD) of larvae caught by benthic sampling (B) or drift sampling (D), and the three hatchery-reared families (round 1 = F1 and F2, round 2 = F3) used for releases during round 2. Only whole intact larvae were weighed. Treatments associated with each site are described in the text, and site N1 is omitted (the one larvae captured at 3 dph was not suitable for weighing). The number of samples used to calculate the mean is indicated in parentheses. Dashed boxes indicate data used in statistical comparisons.

Age (dph)	G1	G2	40m1	40m2	N2	F1	F2	F3
2		B-30.7 \pm 0.6 (3)						
4		B-29.8 \pm 1.3 (8)				23.4 \pm 0.5 (8)	24.7 \pm 0.5 (8)	
6						25 \pm 0.8 (8)	28.3 \pm 0.6 (8)	
7		B-38 \pm 0.5 (8)		B-37.0 (1)				38 \pm 0.5 (8)
8						31.9 \pm 1.1 (8)	32.5 \pm 1.7 (8)	
9								46.8 \pm 4.7 (8)
10						31.1 \pm 0.8 (8)	34.3 \pm 1.8 (8)	
11		B-50.4 \pm 1.4 (8)			B-48.3 \pm 0.6 (3)			48.1 \pm 2.4 (8)
12		D-60.5 \pm 2.1 (8)			D- 46 (1)	39.4 \pm 1.3 (8)	38.9 \pm 1.5(8)	
13		B-54.5 \pm 3.0						47.9 \pm 3.1 (8)
14		D-58.4 \pm 5.7 (5)				38.5 \pm 1.2 (8)	37.5 \pm 2.2 (8)	
15		B-58.3 \pm 3.2 (8)						42.1 \pm 5.8 (8)
16		D-45.7 \pm 2.8 (3)				36.9 \pm 0.6 (8)	38.8 \pm 2.2 (8)	
17		B-52.3 \pm 2.0 (8)						63.4 \pm 7.0 (8)
18			B-42.5 \pm 2.0			39.6 \pm 1.7 (8)	36.4 \pm 1.5 (8)	
19		B-50.9 \pm 4.1 (8)						
20								
21	B-39.7 \pm 3.0		B-39.3 \pm 2.3			47 \pm 8.4 (8)	41.3 \pm 2.9 (8)	
22								
23								
24						76 \pm 14.2 (8)		
25			B-38.7 \pm 0.6					
26								
27								
28						131 \pm 35.4 (8)	100.1 \pm 28.4 (8)	



Figure 5.1 Aerial photo showing the rough location of side channel experimental sites at the spawning reach of the Nechako River near Vanderhoof.

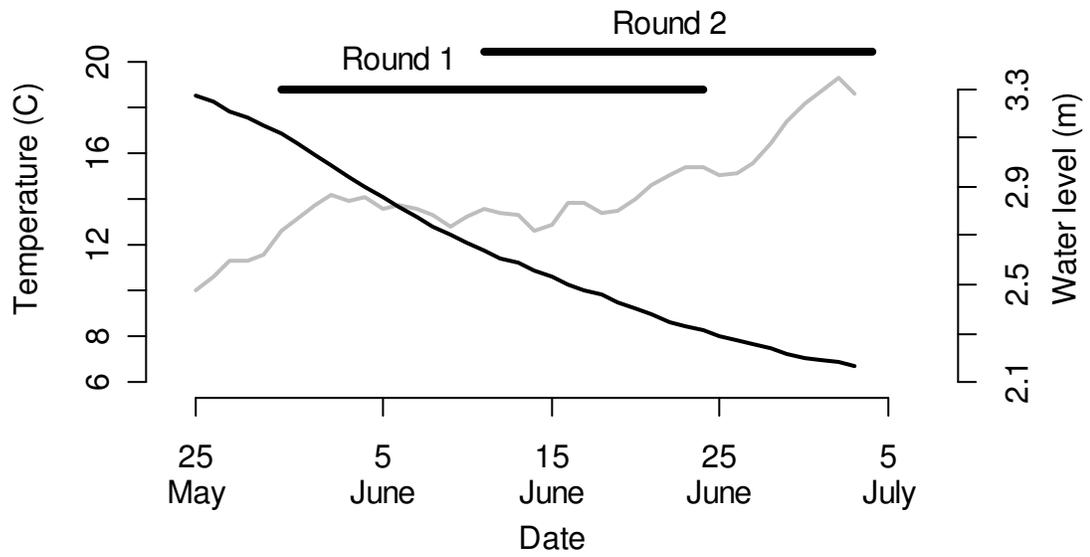


Figure 5.2 Temperature (grey - left axis) and water level (black - right axis) as measured at Vanderhoof WSC station (08JC001) during the experimental period.

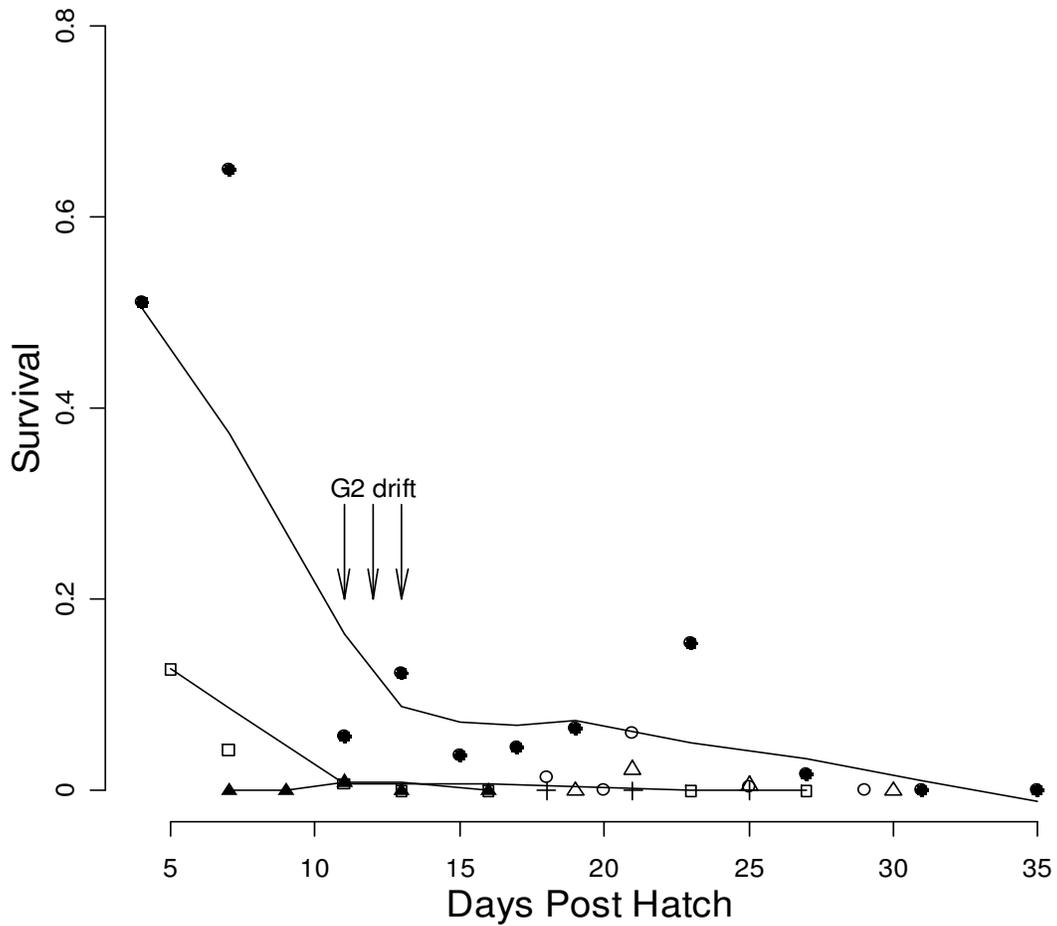


Figure 5.3 Estimated survival of white sturgeon larvae based on benthic sampling of treatment areas for sites G1 (open triangle), 40m1 (open circle), N1 (+), G2 (filled circle), 40m2 (open square) and N2 (filled triangle). Lines are plotted for G2, 40m2 and N2 using the Lowess smoothing algorithm (with settings $f=2/3$ and $\delta=0.3$). Sample sizes vary by treatment and age and are indicated in Table 5.3.

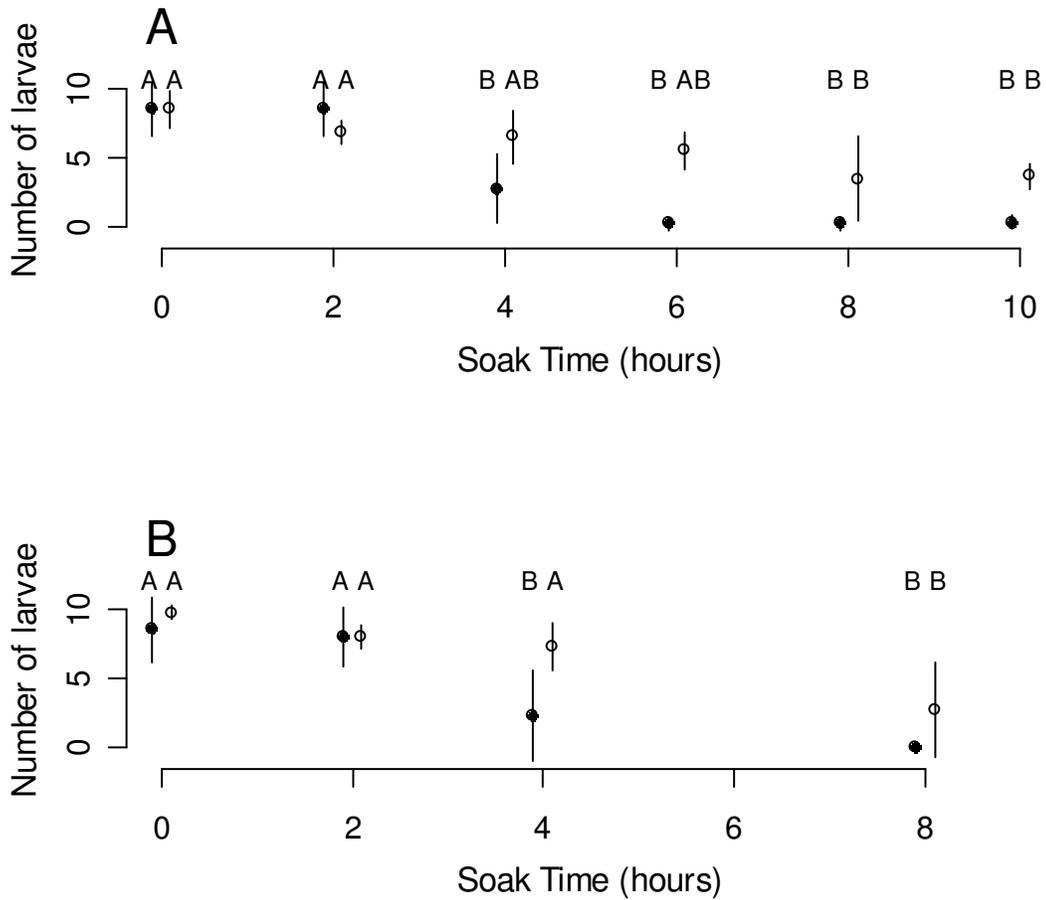


Figure 5.4 Changes in drift net capture efficiency at 1 dph (A) and 12 dph (B) for rectangular (closed symbols) and triangular (open symbols) net configurations (n = 4 for all tests). Superscripts above results indicate statistical differences based on the Tukey multiple comparison test ($p < 0.05$). Note – sampling at six hours was not conducted at 12 dph.

Chapter 6 General Discussion

Identifying links between fish habitat use and population variation presents a substantial challenge (Hayes et al. 2011), and a large amount of research has examined environmental influences on recruitment (Anderson 1988). The present focus on analysis of severe recruitment declines, as distinct from recruitment variation, limits concerns regarding spurious relationships, but cannot eliminate them. However, experimental evaluation of mechanisms by which fine substrates contribute to decreased survival during early life history provide important validation of relationships identified based on hindcasted recruitment. In combination with the identification of egg mortality due to sand inundation (Kock et al. 2006; McDonald et al. 2009), the present results extend the period of substrate mediated effects to include yolk sac larvae (Chapter 3, 4). Substrate change at spawning sites provides a robust explanation for recruitment collapse in white sturgeon based on the weight of evidence from multiple studies. Similarities with other sturgeon (Nichols et al. 2003; Forsythe 2010) and other species (Jennings et al. 2010) suggest such effects may be common amongst large-bodied riverine species. Fortunately, the restriction of impacts to spawning sites suggests that restoration methods identified for lake sturgeon (see Kerr et al. 2010) should provide a basis for white sturgeon restoration using similar methods.

Identification of substrate change as the likely mechanism leading to recruitment collapse contrasts with the common suggestion that multiple factors contribute to recruitment declines (UCWSRI 2002; Williot et al. 2002), and that impacts may even be population specific (UCWSRI 2002; NWSRI 2004). While the possibility that additional factors were involved in recruitment failure cannot be ruled out *a priori*, the Nechako River case study indicates that multiple factors are not necessarily required to explain recruitment collapse. Multi-causal hypotheses for sturgeon recruitment collapse may be based on the understanding that multiple environmental influences affect recruitment variation (Anderson 1988). However, it is important to note that persistently depressed recruitment is more

representative of a habitat regime change because variation is expected to be inconsistent and therefore should not result in consistently low recruitment (unless its extreme variation akin to a regime change). With regard to the upper Columbia River, the abundance of anthropogenic changes is the probable origin of the idea that recruitment declined due to cumulative effects (UCWSRI 2002). However, the present analysis shows that recruitment collapse can be reasonably explained by substrate change alone, and suggests that mitigation efforts should be focused on substrate restoration. With respect to other sturgeon populations it may indeed be impossible (Williot et al. 2002) to identify causes of decline in some cases; however, the present analysis suggests such assumptions should be challenged.

Recruitment hindcasting should be considered an exploratory approach for the identification of potential environmental effects (Catalano et al. 2009). In the two case studies examined here, the use of virtual population analysis and the identification of discontinuities in recruitment time series provided important insight into the apparent timing and cause of recruitment decline, and potential mechanisms were successfully validated by further experiments. With respect to the suitability of such an approach for other species, it is important to note that successful application of these methods was dependent on the availability of substantial population-specific data. Environmental data related to substrate conditions might not be available in many cases. However, historical air photos are often available and provided useful information in Chapter 2. Sufficient age data might also not be available in all cases; however, age structure derived from length data (which is more widely available) may provide a suitable proxy in the presence of distinct recruitment declines (McAdam unpubl.).

Stock structure was also a fundamental component of the present analysis, but can be more challenging to identify. A single stock was assumed in the Nechako River based on the detection of only one spawning site (Liebe et al. 2009) and the population being in Hardy-Weinberg equilibrium (Nelson

et al. 1999; Smith et al. 2002). In contrast, the absence of Hardy-Weinberg equilibrium within the upper Columbia River (Nelson et al. 1999) led to subsequent identification of population genetic structure (Nelson and McAdam 2012). The capability of long-range movements by sturgeon may suggest that localized population structure is unexpected. However, Pacific salmon provide multiple examples demonstrating that long-range movement does not preclude local population structure (e.g., Quinn et al. 2010, 2012), and localized population structure has also been identified for shortnose sturgeon (*A. brevirostrum*; Cooke et al. 2004). Within the unimpounded Fraser River both genetics (Nelson et al. 1999; Smith et al. 2002) and restricted movement (R. L. & L. 2000) identified local populations of white sturgeon in reaches as short as 60 km (from Hope to Yale). Considering that white sturgeon in the upper Columbia River historically had access to over 600 km of contiguous habitat, the presence of stock structure is not surprising. However, over 15 years of research was conducted prior to recognizing this and multiple indicators were required to provide sufficient evidence. Evaluations based on a variety of methods is preferred (Begg and Waldman 1999; Cadrin et al. 2005), and in the present case even the minimum data requirement of a substantial set of recapture data for individually marked fish was collected over fifteen years.

Localized habitat use by discrete stocks contradicts the assumption of panmixia, which is the basis of current white sturgeon management in the upper Columbia River, and this dichotomy could lead to a variety of conservation risks. The absence of complete reproductive mixing between stocks means the effective population size would be lower than when a panmictic population with census estimate of over 3,000 fish is assumed. Additionally, focusing conservation efforts on numerically larger stocks may contribute to the extirpation of smaller stocks, in particular the BRL stock. Because demographic differences between stocks can reflect habitat effects, restoration at individual spawning locations would also have stock-specific effects and would lead to a restricted distribution of newly-recruited fish. For example, demographic distinctions between the WAN and HLK stocks suggest that

restoration at the Waneta spawning site may lead to localized recruitment (similar to the years between 1970 and 1977), but would not lead to population increases in upstream areas. This outcome is predictable based on current data, and suggests that even with successful recruitment restoration at one location, the species' range may still markedly decrease within Canada.

Consideration of the spatial patterns of habitat use also highlights a key assumption in Chapter 3, which is that recruitment is a response to environmental conditions within the spatial area used to define stocks. This assumption is supported by the presence of high fidelity for each stock to its geographic location (greater than 90% of radio tag detections occurred within specified areas – Nelson and McAdam 2012). Demographic differences between the HLK, WAN and ROOS stocks also support this assumption. While contemporary movements between areas during the spawning period suggest the potential breakdown of historical reproductive segregation, demographic patterns should still reflect biological mechanisms that lead to habitat fidelity. For example, though fish from the HLK stock (see Golder 2006b) and ROOS stocks (see Howell and McLellan 2009, 2011) may spawn at the Waneta spawning site, based on the long-term maintenance of demographic differences their progeny would currently be expected to recruit to the WAN stock. While contemporary spawning movements may suggest reproductive mixing, historically reproductive mixing could not have existed historically due to identified genetic differences between stocks (Nelson and McAdam 2012).

With regard to the mechanisms by which localized population structure is created and maintained, the present suggestion that rapid and sustained hiding by yolk sac larvae should occur at spawning sites has important implications. The presence of genetic population structure derived from spatially separated spawning sites (Welsh et al. 2009) implies the presence of natal homing. While imprinting mechanisms have been widely studied in salmonids, studies for sturgeon are limited to Russian sturgeon (*A. gueldenstaedtii*) for which the apparent imprinting 'window' occurred during the

early larval period (Boiko and Grigor'yan 2002). Successful hiding at spawning sites therefore has important implications for subsequent spawning site selection. Increased dispersal in response to the duration of hatchery rearing in lake sturgeon (Crossman et al. 2011) also suggests that there may be effects of both larval and juvenile rearing conditions on subsequent habitat use.

The effects of substrate conditions on the growth and physiology of sturgeon larvae represent a relatively new area of research, although similar effects have been observed in salmonids (e.g., Peterson and Martin-Robichaud 1995). For example, Gessner et al. (2009) showed that Atlantic sturgeon provided with gravel substrate during the yolk sac phase showed increased growth, and similar effects have now been repeatedly observed in white sturgeon both in laboratory (Boucher 2012; McAdam unpubl.) and in field studies (Chapter 5; Crossman and Hildebrand 2012). Substantial differences in larval survival, stress response and fatty acid composition have now also been detected in response to substrate conditions experienced during the yolk sac larval phase (Zubair et al. 2011; Boucher 2012; Baker et al. unpubl.). Similar to other species (see Pechenik 2006), increased energy expenditure due to swimming when complex substrate is absent may explain this effect; however, the shorter time to mortality of unfed versus fed larvae (Boucher 2012; McAdam unpubl.) suggests other mechanisms are involved. Changes in the brain structure and behaviour of rainbow trout (*Oncorhynchus mykiss*) in response to the presence of substrate during early life history (Kihlslinger and Nevitt 2006) indicate the potential for longer-term effects, and, for example, Kerr and Secor (2010) suggest that early life history experience may affect which life history strategy is adopted. As a result, the early rearing environments in captivity may have important implications with respect to the use of fish culture to supplement wild populations.

Identification of multiple additional benefits of interstitial habitat use by yolk sac larvae, in addition to direct effects on survival, emphasizes the need to resolve the dichotomy between drift and

hiding for other sturgeon. Verification of the importance of interstitial hiding for Atlantic sturgeon (Gessner et al. 2009), lake sturgeon (Auer and Baker 2002; Forsythe 2010) and white sturgeon (present study) suggests it is a broader phenomenon that may be shared by all sturgeon. Repetition of similar experiments with other species is therefore recommended. Inclusion of more rigorous experimental procedures, including appropriate replication, is also imperative because comparisons among species continue to be made based on progeny from a single set of parents (e.g., Kynard et al. 2010). Because drift and hiding lead to very different restoration needs, a more complete understanding of larval habitat use has important implications. For example, if current assumptions regarding drift by pallid sturgeon (e.g., Braaten et al. 2008) are incorrect, and pallid sturgeon yolksac larvae also undertake interstitial hiding, the present focus on obligate drift in recovery programs may increase conservation risk for this highly endangered species.

The final chapter in the thesis undertook a small-scale habitat restoration experiment and demonstrated increased yolksac larvae survival in response to substrate augmentation. While spawning substrate restoration has also been effective for lake sturgeon (see Kerr et al. 2010), it is important to note that continued anthropogenic change in affected watersheds may make restoration more complex than simply reversing past changes to spawning habitat. For example, subsequent upstream impoundments in the UCR (Mica Dam 1974, Revelstoke Dam 1983) changed the thermal regime at the Revelstoke spawning site. Decreased summer water temperatures at that site now lead to later spawning and slower larval development (Tiley 2006; Crossman and Hildebrand 2012). While experimental substrate restoration at that location increased larval retention and growth, the number of feeding larvae produced was still low relative to the expected larval production from natural spawning (Crossman and Hildebrand 2012). The combination of density-dependant effects (Justice et al. 2009) and the abundance of hatchery-produced juvenile white sturgeon may also complicate the restoration of wild recruitment. Such examples (see also Dumont et al. 2011) are important reminders

that recruitment dynamics are complicated, and expected responses may not be achieved in some cases.

The delayed recruitment declines of the WAN stock due to its tributary spawning location also has important implications for both causes of decline and habitat restoration. Tributaries have been recognized as important sources of continued variation in regulated rivers, and may play an important role in restoration (Moyle and Mount 2007). The sustained demographic differences between two stocks occupying the transboundary reach (HLK and WAN stocks) present a possible analog for recruitment differences between pallid sturgeon and shovelnose sturgeon, which suggests that recruitment differences between those species may result from differences between mainstem and tributary effects. Identification of tributary influences on paddlefish recruitment (Pracheil et al. 2009) also supports this possibility. Differentiation between mainstem and tributary spawning stocks also provides interesting insight because tributary spawning (e.g., WAN stock, Willamette River -Chapman and Jones 2011) coupled with high fidelity to restricted riverine habitats may provide the basis for distinct reproductive units within spatially structured populations.

The results presented in Chapters 2 and 4 in particular have already provided important support and guidance for habitat restoration tests in the Kootenai (Neufeld and Rust 2007), Columbia (Crossman and Hildebrand 2012) and Nechako rivers (Williamson and McAdam unpubl.), and the rapidity with which research results have been implemented in recovery programs is encouraging. However, rapid infilling after recent substrate augmentation experiments in the Nechako and Columbia Rivers (Cory Williamson, B.C. Ministry of Environment, pers. comm.; Crossman and Hildebrand 2012) emphasizes the challenge presented by restoration of mainstem habitats. These results indicate that restoration in tributaries and dam tailraces offers important advantages due to the decreased inputs of fine substrates.

Prior to conducting this research, the greatest challenge to recovery programs was the identification of the apparent causes of recruitment collapse. Identification of substrate change at spawning sites as the primary cause of historical recruitment declines will hopefully allow debates about sturgeon recruitment declines to move from small-scale restoration to larger, more permanent habitat restoration focused on substrate improvement. While habitat restoration in large rivers will be challenging, the present study should substantially reduce the biological uncertainty regarding the necessity of such measures. In conjunction with other studies (e.g., Dumont et al. 2011; Crossman and Hildebrand 2012) the results of my thesis should also provide important insights that can improve the effectiveness of restoration.

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