

**GROWTH AND SURVIVAL IN THE EARLY LIFE HISTORY STAGES OF WHITE
STURGEON (*Acipenser transmontanus*)**

by

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Abstract

Several populations of white sturgeon (*Acipenser transmontanus*) are experiencing chronic recruitment failure, likely due to low survival in the early life history stages. Despite great conservation interest, knowledge gaps about the basic biology of the early life history stages persists. My first objective was to investigate how periods of starvation after the exhaustion of the yolk sac and the presence of substrate during the yolk sac stage affect growth and survival of the larval stages. I reared newly hatched larvae at 7 levels of starvation after yolk exhaustion (0, 3, 6, 9, 12, 15, and 18 days of starvation). Yolks were exhausted at 11 days post-hatch (dph). After the starvation period, larvae were fed *ad libitum* to 35 dph. Larvae reared in substrate during the yolk sac stage were 12% heavier in wet mass and 27% heavier in dry mass at the end of the stage (11 dph) than larvae reared without substrate. Masses were not significantly different at 35 dph, after 24 days of feeding. Larval mortality rates were not affected by substrate presence or starvation duration. For starvation resistance, all larvae gained wet mass regardless of starvation duration. However, larvae that faced nine or more days of starvation lost dry mass over the study period, indicating that dry mass may be a better metric of growth for larval sturgeon. My second objective was to examine the effect of fish density and food ration on the growth and survival during the early juvenile stage. I reared 2.5-month-old juveniles at four densities (1, 3, 5, or 7 fish/tank) and two ration levels (50% or 100%) for four weeks. Specific growth rate in the first week was 0.69 ± 1.45 %/day for the fish that survived, and -1.19 ± 0.82 %/day for fish that died. Fish that survived for the duration of the experiment grew at 1.94 ± 0.97 %/day over four

weeks, regardless of density or ration treatment. Density significantly and positively influenced the mortality rate, but ration did not. My results indicate that abundant food is critical to the success of white sturgeon in the first year of life.

Lay Summary

In Canada, three of the six populations of white sturgeon (*Acipenser transmontanus*) are experiencing severe declines, and low survival during the early life stages appears to significantly influence population dynamics. Very little is known about the biology of white sturgeon during their first year of life, and the exact cause of low survival is unknown. In this thesis, I performed two studies to examine growth and survival of young white sturgeon. I found that larvae (0-35 days old) are highly resistant to long periods of starvation but have the best growth outcomes when they are not starved. I also found that juveniles (2.5-3.5 months old) compete for limited food resources, and weak competitors are excluded from feeding opportunities. Survival rate decreased with increasing numbers of competitors. My results show that abundant food is critical to the success of young white sturgeon.

Preface

This project was completed in collaboration with the BC Ministry of Environment and Climate Change Strategy. I was responsible for research design, data collection and analysis, and thesis preparation. I was provided guidance and supervision from my co-supervisors Dr. John S. Richardson and Dr. Steve McAdam. Procedures related to the transport, handling and care of experimental animals were approved by the University of British Columbia Animal Care Committee (AUP #A18-0264). Georgia Hall, Vahab Pourfaraj and Teresa Silverthorn assisted with animal husbandry. The Nechako White Sturgeon Recovery Initiative provided the experimental animals and guidance on animal husbandry. Versions of Chapters 2 and 3 will be submitted for publication with the following authorship: Angie Coulter, Steve McAdam, and John S. Richardson.

Table of Contents

Abstract	iii
Lay Summary	v
Preface	vi
Table of Contents	vii
List of Tables	ix
List of Figures	x
List of Abbreviations	xiii
Acknowledgements	xiv
Chapter 1: Introduction	1
1.1 The Order Acipenseriformes.....	2
1.2 White Sturgeon Life History and Conservation Status in Canada	4
1.3 Thesis Overview and Research Objectives	9
Chapter 2: The Critical Feeding Period and the Point of No Return in Larval White Sturgeon	11
2.1 Introduction	11
2.2 Methods	15
2.2.1 Husbandry	15
2.2.2 Experiment Design	17
2.2.3 Growth Measures	17
2.2.4 Statistics	19
2.3 Results.....	20

2.3.1	Influence of Substrate on Growth and Larval Condition	20
2.3.2	Influence of Periods of Starvation on Growth and Larval Condition	24
2.4	Discussion	31
2.4.1	Substrate Improved Growth in Larval White Sturgeon	31
2.4.2	Starvation Decreased Growth and Health Metrics of Feeding Larvae	35
2.4.3	Evidence for the Point of No Return	37
2.4.4	Evidence of Larval Starvation in the Wild and its Contribution to Recruitment Failure.....	39
Chapter 3: Growth and Intraspecific Competition of Age-0 White Sturgeon		43
3.1	Introduction	43
3.2	Methods	46
3.2.1	Broodstock.....	46
3.2.2	Husbandry	46
3.2.3	Experiment Design	47
3.2.4	Calculation of Optimal Feeding Rate	49
3.2.5	Statistics	50
3.3	Results.....	52
3.4	Discussion	58
Chapter 4: Discussion		69
4.1	Implications and Future Directions	72
References.....		77

List of Tables

Table 3.1 Comparison of three optimum feeding rate (OFR, % body mass/day) models for the mean and range of initial masses of juvenile white sturgeon used in this experiment (1.785-5.687 g).....	50
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List of Figures

Figure 2.1 A) Wet mass and B) dry mass of larval white sturgeon (<i>Acipenser transmontanus</i>) reared with and without substrate at 11 and 35 days post-hatch. The boxplot represents the median and 25 th and 75 th percentiles. The whiskers represent the smallest and largest values within 1.5 times the inter-quartile range of the percentile boundaries. ‘*’ indicates a statistical significance level of $p < 0.05$. ‘NS’ indicates the difference is not statistically significant.	22
Figure 2.2 Specific growth rates of larval white sturgeon (<i>Acipenser transmontanus</i>) reared with and without substrate as measured by wet and dry mass over 35 days post-hatch. The dashed line indicates a growth rate of zero.....	24
Figure 2.3 A) Wet mass and B) dry mass (mg) of larval white sturgeon (<i>Acipenser transmontanus</i>) at the end of the study period (35 days post-hatch; dph). Delayed initiation of feeding was negatively related to final wet mass.....	25
Figure 2.4 Tissue water content (%) of larval white sturgeon (<i>Acipenser transmontanus</i>) at the end of the study period (35 days post-hatch; dph). Water content was positively related with day of initiation of feeding.	26
Figure 2.5 Fulton’s condition factor, K, of larval white sturgeon (<i>Acipenser transmontanus</i>) at the end of the study period (35 days post-hatch; dph). Poor condition was related to increasing days of starvation.	27
Figure 2.6 Specific growth rates of larval white sturgeon (<i>Acipenser transmontanus</i>) that survived to the end of the study period (35 dph) measured by A) wet mass and B) dry mass. The dashed line indicates zero growth over the study period.	29

Figure 2.7 Mean growth trajectories of larval white sturgeon (*Acipenser transmontanus*) between 11 and 35 days post-hatch (dph) measured in A) wet mass and B) dry mass. Treatment denotes the day of initiation of feeding, with “B” representing larvae reared without substrate in the yolk sac stage and feeding initiated at 11 dph. A single larva was randomly selected for weighing from each tank in three-day intervals from 11 dph to 35 dph. 30

Figure 3.1 The specific growth rate of juvenile white sturgeon during the first week of the experiment. The survival outcome, whether the fish survived for the duration of the experiment or died in the subsequent weeks of the study, significantly influenced the growth rate. Fish that survived for the duration of the four-week experiment (n=72) grew significantly more than fish that died in weeks two to four (n=24). The boxplot represents the median and 25th and 75 percentiles. Whiskers are the smallest and largest values within 1.5*IQR of the percentile value. The dashed line indicates a growth rate of zero. 53

Figure 3.2 Per-tank growth efficiency of juvenile white sturgeon over the four-week experiment duration. Fish in treatments that were fed at half ration grew significantly more efficiently than tanks fed full rations. Density did not have a significant effect. Bands indicate the 95% confidence interval. 54

Figure 3.3 Mortality rate per tank of juvenile white sturgeon over the four-week experiment duration. Mortality rate significantly increased with tank density. Bands indicate the 95% confidence interval..... 55

Figure 3.4 Final mass of the juvenile white sturgeon that A) survived to the end of the four-week study period and B) did not survive to the end of the four-week study period.

Final mass was best predicted by the initial mass in both linear models. Bands indicate the 95% confidence interval. 57

List of Abbreviations

dph Days post-hatch

DU Designatable unit

FL Feeding larvae

OFR Optimal feeding rate

PNR Point of no return

SARA Species at Risk Act

SGR Specific growth rate

YSL Yolksac larvae

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Chapter 1: Introduction

Freshwater ecosystems and the biodiversity they host are integral to the prosperity of human societies and provide innumerable ecosystem services. Our demands for many of these services, including drinking water, food, transportation, and energy generation, are unsustainable and are leading to severe impacts on freshwater biodiversity globally (Aylward et al. 2005; Dudgeon 2010). Freshwater biodiversity has historically been threatened by five major anthropogenic stressors: overexploitation, habitat degradation, flow modification, pollution and species invasions (Dudgeon et al. 2006). However, the Anthropocene is increasingly introducing novel threats to biodiversity worldwide, with freshwater biodiversity disproportionately threatened compared to marine and terrestrial ecosystems (Reid et al. 2019). In North America, freshwater fauna extinction rates are four times higher than terrestrial fauna and three times higher than coastal marine mammals (Ricciardi and Rasmussen 1999). Urgent and widespread efforts are needed to alter the business-as-usual trajectory of rapid biodiversity loss and conserve the vital services that freshwaters provide (Tickner et al. 2020).

Freshwater ecosystems account for less than 1% of the Earth's surface, yet host approximately 10% of total animal species and one-third of all vertebrates recognized globally (Balian et al. 2008; Strayer and Dudgeon 2010). In addition to these animals, freshwaters are home to 1% of the world's vascular plants, and innumerable micro-organisms. This is likely a gross underestimate of the biodiversity of freshwaters, as they are poorly represented in the conservation biology literature (Strayer and Dudgeon 2010). Of the 126,000 animal species estimated to occupy freshwaters, approximately

13,000 species are fish (Lévêque et al. 2008). These species represent 2,513 genera and account for over 45% of global fish diversity (Lévêque et al. 2008).

1.1 The Order Acipenseriformes

One such group that exemplifies the challenge of the management and conservation of freshwater fish is the Order Acipenseriformes, the sturgeons and paddlefish.

Acipenseriforms are regarded as “living fossils” and have existed since at least the Lower Jurassic, approximately 200 million years before present (Gardiner 1984; Bemis et al. 1997). They have undergone few morphological changes since the origins of the order and have evolved slower than contemporary teleost fishes (Krieger and Fuerst 2002). Acipenseriforms are characterized by large, scaleless bodies with cartilaginous skeletons, and exhibit long-lived, slow-maturing life histories (Pikitch et al. 2005). The order is made of two families, the sturgeons (Acipenseridae) with 25 extant species, and the paddlefish (Polyodontidae), with a single extant species (Haxton et al. 2016; Zhang et al. 2020).

Acipenseriforms occupy large rivers, lakes, estuaries, nearshore ocean, and inland seas in the northern hemisphere (Pikitch et al. 2005). All species require freshwater to spawn and for rearing during their early life stages, and employ anadromous, amphidromous, or potadromous life histories (Bemis and Kynard 1997). The adults spawn over coarse rock substrates, though depth and velocity of spawning areas vary between species (Haxton et al. 2016). The adults release their gametes into the water column without building a nest; upon release, eggs become adhesive with exposure to freshwater and

sink to stick to the substrate (Scott and Crossman 1973; Cherr and Clark 1985). After maturation, adults spawn iteroparously, though the females do not spawn every year (Bemis and Kynard 1997). Spawning events occur in spring or summer, when water temperatures are under 20 °C (Dettlaff et al. 1993). Juveniles of anadromous and amphidromous species have limited salinity tolerances and live in fresh or brackish water for the first several years of their life before being able to tolerate the salinity of seawater habitats (Cech and Doroshov 2005).

Long-lived freshwater fish are particularly vulnerable to anthropogenic stress and extinction (Olden et al. 2007). Their unique life history characteristics, particularly their late maturation and periodic reproduction cycles, make them vulnerable to anthropogenic stressors leading to high levels of endangerment in North America and across the globe (Pikitch et al. 2005; Jelks et al. 2008). Sturgeon and paddlefish are among the most endangered fish in the northern hemisphere (Pikitch et al. 2005). All 26 species are listed on the IUCN Red List, with 63% classified as critically endangered (Haxton et al. 2016). Local extinctions have been observed for 19 of 26 species, and four species may now be extinct in the wild (Birstein 1993; Zhang et al. 2020).

Increasing industrialization in the late 1800s and early 1900s led to declines in acipenseriforms globally (Auer 2005). Overharvesting by commercial fishing for meat and caviar drove steep declines in populations and few viable sturgeon fisheries remain active today (Pikitch et al. 2005). Illegal harvest remains a serious threat to adult sturgeon, with sophisticated poaching rings in operation (Israel et al. 2009).

Concurrently, habitat alteration and destruction are reducing the availability of vital

habitats. The installation of mainstem dams for hydroelectric power generation has caused profound changes to sturgeon riverine habitat. Dams have contributed to habitat fragmentation and have altered temperature, sediment and flow regimes (Haxton and Cano 2016). Additionally, logging and mining industries have contributed to the destruction of river and riparian habitat, and increased water pollution (Auer 2005).

1.2 White Sturgeon Life History and Conservation Status in Canada

White sturgeon (*Acipenser transmontanus*) is North America's largest and longest living freshwater fish, with specimens reported over 6 meters in total length and over 100 years old (Scott and Crossman 1973). Their coastal range extends from Baja California in northern Mexico to the northern Gulf of Alaska, occupying large rivers in the Fraser, Columbia, Sacramento and San Joaquin basins (Ruiz-Campos et al. 2011; Hildebrand et al. 2016). Details of the marine movements of white sturgeon are largely unknown, with the majority thought to remain in the river with brief trips to ocean (Galbreath 1985). However, observations of large-scale marine movements between river basins have been recorded (Welch et al. 2006). Sexual maturity in white sturgeon begins at approximately 12 years old in males and between 15 and 32 years old in females (Hanson et al. 1992). Estimates of spawning intervals vary between 3 and 11 years, with the interval length increasing with age (Hildebrand and Parsley 2013; Fisheries and Oceans Canada 2014). Once mature, adults reproduce across their lifespan, with no evidence of reproductive senescence (Paragamian et al. 2005; Hildebrand et al. 2016).

The early life history consists of the egg incubation, yolksac larvae and feeding larvae stages. Adults aggregate to spawn between February and August (Hildebrand et al. 2016). The embryos incubate for 11 to 14 days, depending on temperature, and then hatch from the egg casing (Boucher et al. 2014). Larvae emerge from the egg with an endogenous yolk sac, a nutritional reserve attached to their ventral surface. After emerging from the egg, the yolksac larvae (YSL) hide in interstitial spaces in coarse substrates (McAdam 2011). Once the yolk has been nearly depleted, the larvae must begin to feed exogenously on freshwater invertebrates (Muir et al. 2000). Exogenous feeding is initiated at 8 to 14 days post-hatch (dph), just prior to the complete absorption of the yolk (Conte et al. 1988). Once the yolk sac is absorbed, feeding larvae (FL) emerge from the substrate and drift downstream (McAdam 2012). At approximately 40 dph, FL develop features of the adult morphology and metamorphose into the early juvenile stage (Buddington and Christofferson 1985).

Four of six Canadian populations have been legally listed as endangered under the Species at Risk Act (SARA) since 2006 (Fisheries and Oceans Canada 2014). In 2012, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) reclassified the Nechako, upper Fraser and middle Fraser populations into one Upper Fraser management unit (designatable unit, DU) due to insufficient genetic differentiation between the three regions (COSEWIC 2012). However, there is evidence that the three populations remain genetically distinct despite some range overlap (Smith et al. 2002; Schreier et al. 2013). Detailed historical population information is sparse for all

populations in Canada as research efforts have been limited until recent years (Fisheries and Oceans Canada 2014).

Recruitment, the addition of new individuals joining a population each year, is a vital component of self-sustaining populations. Chronic recruitment failure, where juvenile survivorship is below the population replacement rate, is responsible for the continued decline in white sturgeon population numbers (COSEWIC 2012). Recruitment levels in the Nechako, Columbia and Kootenay rivers are at historic lows, with extremely rare observations of naturally spawned young-of-the-year in the wild (COSEWIC 2012). Regulation of flow on these rivers is a common feature, with recruitment crashing after the construction of a mainstem dam (Fisheries and Oceans Canada 2014). Previous work has identified that recruitment failure appears to be caused by high rates of mortality in the early life history stages (McAdam 2015; Hildebrand et al. 2016). Modification of flow has led to shifts in geomorphological regimes, resulting in alterations of riverbed composition. Evidence of sediment alterations to spawning reaches has been found in all three rivers, with fine sediments infilling the interstitial spaces between coarse substrates that larvae historically occupied (Blair and McPherson 1999; Paragamian et al. 2001; McAdam et al. 2005; McAdam 2015). Though flow regulation alters many habitat characteristics, geomorphology alterations are the suspected drivers of decreased survival in the egg and YSL life history stages due to smothering and insufficient interstitial hiding habitat, respectively (Kock et al. 2006; McAdam 2011, 2012; Boucher et al. 2014).

The Fraser River and its tributaries are home to four of the six white sturgeon populations in Canada. Due to the extensive effort required for population monitoring, trends are not well established, and the abundances of juveniles are unknown for most populations. The Upper Fraser DU has an estimated 1,564 adult fish, consisting of 185 in the Upper Fraser, 749 in the Mid-Fraser, and 630 in the Nechako River population segments (Fisheries and Oceans Canada 2016). Trend data are unavailable for the Mid- and Upper Fraser populations, but they are considered to be at or near historic levels due to their stable age structure and absence of known threats in the regions (Ptolemy and Vennesland 2003). The Nechako River population has been declining due to recruitment failure since 1967, following the installation of the Kenney Dam in 1952 (McAdam et al. 2005). A conservation hatchery was established in 2014, but post-release mortality of hatchery juveniles is high. Preliminary findings show that one-year post-release survival is poor, with radio tagged juveniles experiencing 56-78% mortality (Nechako White Sturgeon Recovery Initiative 2020). Predation pressure by river otters (*Lutra canadensis*) is a contributing factor to poor survival, with 523 PIT tags and 25 radio tags from Nechako hatchery fish found in latrine sites to date. The Lower Fraser River is not impounded by a mainstem dam, and the population appears to continue recruiting successfully. However, the population is in decline. Abundance estimates of 60 to 279 cm fork length (FL) white sturgeon (Age 7-55) have declined from 61,135 in 2003 to 29,858 in 2019, with the decline driven by a 78% reduction in the number of juveniles (60-99 cm FL)(Nelson et al. 2020). This decline has been attributed to habitat loss and reduction in prey availability, as much of the estuary, floodplain and side

channel habitats used by young juveniles have been lost or disconnected from the mainstem river (Fisheries and Oceans Canada 2014).

The Nechako River population is not alone in experiencing declines in apparent recruitment rates. The Upper Columbia River population is a transboundary population that extends from the Revelstoke Dam in British Columbia to the Grand Coulee Dam in Washington. Recruitment failure began in approximately 1968, coinciding with the installation of mainstem dams, and continues to affect the Upper Columbia River population (McAdam 2015). In 2003, the wild white sturgeon abundance was estimated at approximately 3,000 fish with large adult fish making up the majority of the population (Irvine et al. 2007; Fisheries and Oceans Canada 2014). Extensive conservation hatchery releases of larvae and early juveniles have increased the abundance of juveniles to approximately 22,124 as of 2012 (Hildebrand and Parsley 2013). The Kootenay River (spelled 'Kootenai' in the United States) population is also a transboundary population and extends from Kootenai Falls, Montana to Duncan Dam in British Columbia. Following the construction of the Libby Dam in Montana, little to no recruitment has happened since 1965 (Paragamian 2012). Wild adult white sturgeon are declining in abundance, decreasing from 2,072 individuals in 2011 to 1,744 individuals in 2017 (Hardy and McDonnell 2019). Hatchery supplementation of juvenile white sturgeon in the Kootenai River began in 1992, resulting in an estimated 12,000 juvenile and sub-adults added to the population as of 2013 (Dinsmore et al. 2015).

1.3 Thesis Overview and Research Objectives

This thesis addresses the general objective of generating knowledge to help fill two of four knowledge gaps identified in the SARA recovery strategy for white sturgeon in Canada: (1) basic biological information on the early life history stages of white sturgeon and (2) knowledge of factors contributing to ongoing recruitment failure (Fisheries and Oceans Canada 2014). I used laboratory experiments to test fundamental ecological questions of growth and survival in the early life history stages of white sturgeon. A thorough understanding of the biology of the early life history stages is critical to population recovery efforts, but these stages have historically been difficult to study in the wild (COSEWIC 2012).

Chapter 2 details an experiment conducted to investigate the growth and survival of the larval life history stages. By manipulating substrate and timing of availability of food resources, I attempted to answer the following questions: (1) Does the presence of substrate during the YSL period influence the growth and survival of YSL and FL? and (2) How long is the critical period for white sturgeon and when is the point of no return (PNR), the point at which larvae cannot recover from starvation despite an abundance of food? I predicted that the presence of substrate would have a positive effect on growth and survival in the YSL and FL stages. Coarse substrates allow YSL to hide in interstitial spaces rather than constantly swimming in the water column. Therefore, YSL in substrate should be able to allocate more of their endogenous yolk reserves for growth and development (Boucher et al. 2014). I also predicted that white sturgeon would have a long critical period to encounter their first feeding before reaching the

PNR, as white sturgeon YSL have large yolk stores and long critical periods have been found in other sturgeon species (Doroshov et al. 1983; Hardy 2000; Chai et al. 2011).

Chapter 3 focuses on growth and intraspecific competition in Age-0 juvenile white sturgeon. I conducted an experiment to test how conspecific density and food ration influences the growth and mortality rates of three-month-old juvenile white sturgeon. The aim of this experiment was to answer the following questions: (1) Do juvenile white sturgeon compete intraspecifically for limited food resources? (2) Does conspecific density limit the growth of juvenile white sturgeon? I predicted that fish experiencing high food availability and low conspecific density would have higher growth rates and lower mortality rates than those at high conspecific densities and low food availability.

In Chapter 4, I synthesized the results of my experiments and discussed the limitations of my research. Finally, I suggest potential directions for future research and examine the implications of my findings for continuing conservation efforts to increase recruitment and restore self-sustaining white sturgeon populations.

Chapter 2: The Critical Feeding Period and the Point of No Return in Larval White Sturgeon

2.1 Introduction

The early life history stages of fishes have been recognized for a century as critically important to the future abundance of a stock, yet for many marine and freshwater species a lack of basic biological information for these stages continues to hamper fisheries management (Hjort 1914; Chambers and Trippel 2012). Hjort's *critical period hypothesis* proposed that the period when larvae transitioned from endogenous feeding on yolk reserves to exogenous feeding is crucial to the recruitment of the cohort (Hjort 1914, 1926). If food quantities and qualities are insufficient, rapid and high mortality is expected. Following the statement of Hjort's hypothesis, identifying the critical period for fish species became a prominent focus of recruitment research (Marr 1956; May 1974; Ellertsen et al. 1995). However, evidence for the existence of this singular critical period for fish larvae and the magnitude of its influence on recruitment remains contentious (as reviewed by Houde 2008). Furthermore, the applicability of the critical period hypothesis to freshwater fish has been questioned (Mookerji and Rao 1999; Rao 2003). In general, marine larvae have smaller body sizes and yolk reserves, higher mortality rates and are less resistant to starvation stress than freshwater fish (Elgar 1990; Houde 1994). Rapidly encountering their first exogenous meal after the absorption of the yolk-sac is vital to their survival; some marine species have been found to have a critical period of 3-5 days before dying of starvation (Yin and Blaxter 1987; Yang 2007). In contrast, freshwater fish generally have larger eggs that allow larvae to have large yolk provisions

and higher starvation resistance (Duarte and Alcaraz 1989). These characteristics afford freshwater larvae longer periods of time to forage for their first exogenous meal and to leave habitat patches that do not have suitable prey available. Therefore, the period to transition to exogenous feeding may be 'less critical' for many freshwater fish. The end of the critical period is marked by the 'point of no return' (PNR), the threshold point at which larvae cannot recover from starvation (Blaxter and Hempel 1963). Once the PNR is surpassed, the larvae are unable to feed even in the presence of abundant food. The larvae will reduce activity and eventually starve to death.

Changes in recruitment-limiting factors, including food availability, habitat degradation, predation pressures, and poor parental condition, can lead to recruitment failure for an entire year class (Anderson 1988). If recruitment failure persists across several reproduction cycles, declines in overall population numbers are expected. This pattern is exemplified in white sturgeon (*Acipenser transmontanus*), a freshwater fish species of conservation concern which is experiencing ongoing recruitment failure in several populations (Fisheries and Oceans Canada 2014). In the Columbia, Kootenay and Nechako rivers, recruitment levels are at historic lows, with very rare observations of naturally spawned young-of-the-year in the wild (COSEWIC 2012). Though the causal mechanisms of recruitment failure in these populations are currently unconfirmed, they appear to be associated with river flow regulation and affect the earliest life history stages of white sturgeon (COSEWIC 2012; Hildebrand et al. 2016). The early life history consists of the egg incubation, yolk-sac larvae (YSL) and feeding larvae (FL) stages. White sturgeon eggs are larger than many freshwater fish species, with an egg diameter

of 3.8-4.0 mm (Doroshov et al. 1983; Duarte and Alcaraz 1989; Elgar 1990). After emerging from the egg, YSL hide in the interstitial spaces of bed substrate in the vicinity of the spawning location (McAdam 2011). Once the yolk is depleted at approximately 12 days post-hatch (dph), the larvae transition to the FL stage (Doroshov et al. 1983; Buddington and Christofferson 1985). At the transition between the YSL and FL stages, white sturgeon appear to use a mixed feeding strategy. Before the yolk reserves are fully depleted, larvae begin to forage for benthic invertebrates (Conte et al. 1988; Hildebrand and Parsley 2013). The FL stage extends from the transition to exogenous feeding to the completion of metamorphosis to the juvenile stage at 40 to 60 dph, when adult features are fully formed (Buddington and Christofferson 1985; Fisheries and Oceans Canada 2014). The importance of the timing of the first exogenous feed during the mixed feeding or FL stage and its implications for recruitment are unknown. The ability to hide during the YSL stage has been shown to be beneficial for growth and survival of white sturgeon YSL and FL (McAdam 2011; Boucher et al. 2014). However, the timing of emergence from the substrate, and whether it is temporally synchronous with the first feeding is undetermined. Sampling of drifting larvae has yielded mixed results, with evidence of both YSL and FL drifting (Muir et al. 2000; Hildebrand and Parsley 2013; Crossman and Hildebrand 2014). Additionally, white sturgeon larvae disperse via downstream drift after emergence from the substrate. The distance and duration of drift is unknown, but the swimming intensity of drifting larvae suggest that larvae drift for many days and have been found up to 200 km downstream from known spawning reaches (McCabe and Tracy 1994; Kynard and Parker 2005). This shift in habitat at or near the initiation of feeding makes not only timing of initial feeding

important for recruitment, but also the availability of prey at the location of settlement after downstream drift.

Starvation during the FL stage due to damming-induced changes in productivity and benthic macroinvertebrate abundance and richness has been hypothesized as a contributing factor to recruitment failure in white sturgeon populations (McAdam 2012; Poff and Schmidt 2016). Yet, studies of prey availability and larval starvation have been inconclusive in support of the starvation hypothesis. In Lake Roosevelt on the upper Columbia River, 95% of wild white sturgeon larvae (YSL and FL) captured in benthic plankton nets had empty stomachs (Reihart 2016). Although this may indicate that larvae have not successfully found food, 99% of the larvae caught had not completely exhausted their yolk reserve. This suggests that the larvae may have not fully transitioned to the FL stage prior to drifting and have been captured at a time when conclusions on nutrition status and prey preference are difficult to make. Sampling in this region has consistently yielded results of larvae with yolk reserve remaining at the time of capture (Hildebrand and Parsley 2013). Furthermore, prey items found in the stomachs of white sturgeon FL in other regions (e.g., chironomids and *Hydra*) have been found in abundance in Lake Roosevelt (Hindle 2018). In the lower Columbia River, no evidence of larval starvation has been found (Muir et al. 2000). Nevertheless, investigations on the effects of starvation in white sturgeon FL and their implications for recruitment are warranted as the limitations on recruitment for threatened populations have not been sufficiently tested in the primary literature.

Due to the difficulty of finding white sturgeon FL in the wild at a time that would allow managers to make conclusions about the proportion of FL experiencing starvation and its potential effects on recruitment, I conducted a laboratory study to investigate how growth and survival may be influenced by starvation during the FL stage. The objectives of my study were to 1) determine the influence of availability of interstitial habitat during the YSL stage on the growth and survival of YSL and FL, and 2) investigate the duration of the critical period of transition between the YSL and FL stages and determine the PNR for white sturgeon. YSL in substrate are able to use interstitial areas to hide and allocate more of their endogenous yolk reserves for growth and development rather than swimming in the water column (Boucher et al. 2014). I predicted that the presence of substrate would have a positive effect on growth and survival in the YSL and FL stages. I also predicted that white sturgeon larvae will have a long critical period to initiate feeding after the depletion of yolk due to their characteristic large egg size and corresponding yolk sac, giving foraging FL enough time to find suitable food resources before reaching the PNR (Doroshov et al. 1983).

2.2 Methods

2.2.1 Husbandry

The white sturgeon used in this study were acquired from the Nechako White Sturgeon Conservation Centre in Vanderhoof, British Columbia. Wild, adult white sturgeon were captured for broodstock from the Nechako River in May 2019. Ovulation in female fish was induced on June 3rd, 2019 using a luteinizing hormone-releasing hormone analogue (Syndel Laboratories Ltd., Nanaimo, British Columbia). Eggs were collected

from three females and fertilized with milt collected from eight male fish, resulting in the three maternal families used in this study. After neurulation (developmental stages 18-23; Dettlaff et al. 2012) the embryos were transported in coolers by air freight to the Vancouver campus of the University of British Columbia on June 10th. Upon arrival, the embryos were transferred to a 14 °C environment chamber with a 14L:10D photoperiod in the InSEAS facility in the Department of Zoology. The embryos were held in a 40 L standard glass aquarium (50 cm x 25 cm x 30 cm) filled with dechlorinated municipal water and aerated with an aquarium air stone. Half of the water in the aquarium was exchanged twice per day to maintain water quality. During the water changes, embryos with symptoms of disease for malformation were removed.

On the day of hatch (0 dph; June 13th), 30 YSL were transferred to each of the experimental units. The experiment was conducted in forty 1.2 L, square acrylic containers (approximately 12.5 cm x 12.5 cm x 11.5 cm). The containers were filled with dechlorinated municipal water and aerated with an aquarium air stone. In the treatment groups reared with substrate, a 50:50 mixture by volume of 2.5 cm and 3.8 cm diameter polyethylene bio-balls (Dynamic Aqua-Supply Ltd. Surrey, BC) to approximately 5 cm depth were used as artificial substrate. 'Bio-balls', plastic balls with an open structured pattern to increase surface area for biofilms to develop in aquarium filtration systems, simulate interstitial hiding spaces in coarse substrates they would typically occupy in the wild (Kieselbach 2008; McAdam 2011). In the bare treatment groups, the YSL were reared without substrate. At 11 dph, the first incidence of melanin plug extrusion from the gut was observed, an indication of the onset of the FL stage (Hildebrand et al.

2016). At this time, the substrate was removed from the containers and feeding was initiated for all treatments. FL were fed EWOS® Micro #0 crumble (Cargill, Minneapolis, Minnesota) three times per day *ad libitum*. Any remaining food that was not eaten was removed by siphoning prior to the next feeding. Half of the water in the container was changed once per day to maintain water quality. At each feeding, mortalities were removed and recorded.

2.2.2 Experiment Design

Experimental containers were assigned to one of eight treatment groups: YSL reared with substrate with feeding initiated at 11, 14, 17, 20, 23, 26 or 29 dph, and YSL reared without substrate with feeding initiated at 11 dph, resulting in 5 replicates of each treatment. One fish per experimental container was sampled for growth measures at 0, 11, 14, 17, 20, 23, 26, 29, 32 dph. FL were randomly selected from the containers and were euthanized by immersion in a bath of 200 mg L⁻¹ tricaine methanesulfonate (Finquel MS-222, Argent Laboratories, Redmond, WA) buffered with 400 mg L⁻¹ sodium bicarbonate for 15 minutes. At the end of the experiment at 35 dph, all remaining FL were euthanized using the same protocol.

2.2.3 Growth Measures

Immediately after euthanasia, FL were photographed to measure total length. After photographing, the FL were weighed for wet mass by blotting for excess water using Kimwipes (Kimberly-Clark Professional, Roswell, GA) and air drying for ten seconds prior to weighing on an analytical balance (Sartorius CP124S, accuracy ±0.1 mg;

Goettingen, Germany). After weighing, FL were transferred to 1.5 ml Eppendorf tubes (Eppendorf AG, Hamburg, Germany) and preserved by freezing at -23 °C until the end of the experiment. Dry masses were measured at the end of the experiment by thawing frozen samples at room temperature for 15 minutes before removing samples from the Eppendorf tubes and drying in an oven at 60 °C for 72 hours in aluminum weighing boats.

Using the length and weight measurements, two growth and condition indices were calculated to compare the outcomes of periods of starvation after absorption of the yolk sac and the influence of substrate on larval health. The first growth index calculated was the specific growth rate (SGR)(Equation 2.1; Lugert et al. 2016).

$$SGR = \frac{\ln(w_t) - \ln(w_i)}{t} * 100 \quad (2.1)$$

Where the specific growth rate (%/day) is determined by the difference between the natural logarithm of the final mass (w_t) and the initial mass (w_i) in g over time (days). Growth rates were calculated for the YSL phase (11 days) and the full study period (35 days) for both the wet and dry masses. The difference between wet and dry masses was then used to calculate the water content of the tissues.

The second growth metric was Fulton's condition factor (K), a measure of 'wellbeing' based on the assumption that fish that are heavier for a given length are healthier (Equation 2.2; Froese 2006).

$$K = 100 * \frac{W}{L^3} \quad (2.2)$$

Where Fulton's condition factor (K) is determined by the FL wet mass in grams (W) and total length in centimeters (L).

2.2.4 Statistics

Statistical analyses were conducted in the R programming language (version 3.6.1) in the RStudio environment (version 1.2.5019)(R Core Team 2019; RStudio Team 2019). Data are expressed as mean \pm standard deviation. To compare the growth outcomes of larvae reared with and without substrate, I used a series of Student's t-tests to compare the means of the treatments at 11 and 35 dph to capture growth in the YSL stage and across the study period. To test for violations of the assumptions of homogeneity of variance and normality, I used an *F*-test and a Shapiro-Wilk test of normality, respectively. In the case of unequal variances, I used a Welch t-test as an alternative to the Student's t-test. Hedges' *g*, a measure of effect size for a t-test with small sample sizes, was calculated for each t-test using the *effsize* package (Rosenthal 1994; Torchiano 2020).

To test the effect of periods of starvation on larval growth outcomes, I fit a series of linear regression models. Assumptions of the linear models were tested with the *gvlma* package (Pena and Slate 2006). Outliers were then identified using fitted vs residuals plots and quantile-quantile plots in base R and removed from analyses.

2.3 Results

2.3.1 Influence of Substrate on Growth and Larval Condition

White sturgeon YSL that were reared with substrate were 12% larger than larvae reared without substrate at 11 dph, with wet masses of 31.20 ± 1.99 mg and 27.72 ± 2.16 mg, respectively (Figure 2.1A; $t_{[8]} = -2.65$, $p = 0.03$, $g = 1.51$). After the initiation of feeding at 11 dph, larvae were fed *ad libitum* for 24 days (to 35 dph). At 35 dph, larvae reared in substrate were larger than those reared without, with final wet masses of 60.52 ± 4.86 mg and 55.11 ± 6.17 mg, respectively ($t_{[8]} = -1.54$, $p = 0.16$, $g = 0.88$). Although not statistically significant, larvae reared in substrate were 9% heavier based on wet mass. A similar pattern was found for the dry masses at 11 dph and 35 dph (Figure 2.1B). Based on dry mass larvae reared with substrate were 27% heavier (4.38 ± 0.71 mg) at 11 DPH than larvae reared without substrate (3.44 ± 0.23 mg; $t_{[8]} = -2.81$, $p = 0.02$, $g = 1.60$). At 35 dph, the dry masses were not significantly different, but larvae reared in substrate were 11% heavier ($t_{[8]} = -1.18$, $p = 0.27$, $g = 0.67$). Larvae reared with substrate were 5.45 ± 0.50 mg and larvae reared without substrate were 4.89 ± 0.94 mg.

Fulton's condition factor, K , was not significantly different between larvae reared with and without substrate at 11 dph and 35 dph. At 11 dph, K was 0.61 ± 0.07 for larvae reared in substrate and 0.60 ± 0.05 for larvae reared in bare tanks ($t_{[8]} = -0.20$, $p = 0.85$, $g = 0.11$). K was lower at 35 dph, with larvae reared with and without substrate at a K of 0.48 ± 0.02 ($t_{[8]} = 0.34$, $p = 0.7392$, $g = 0.20$).

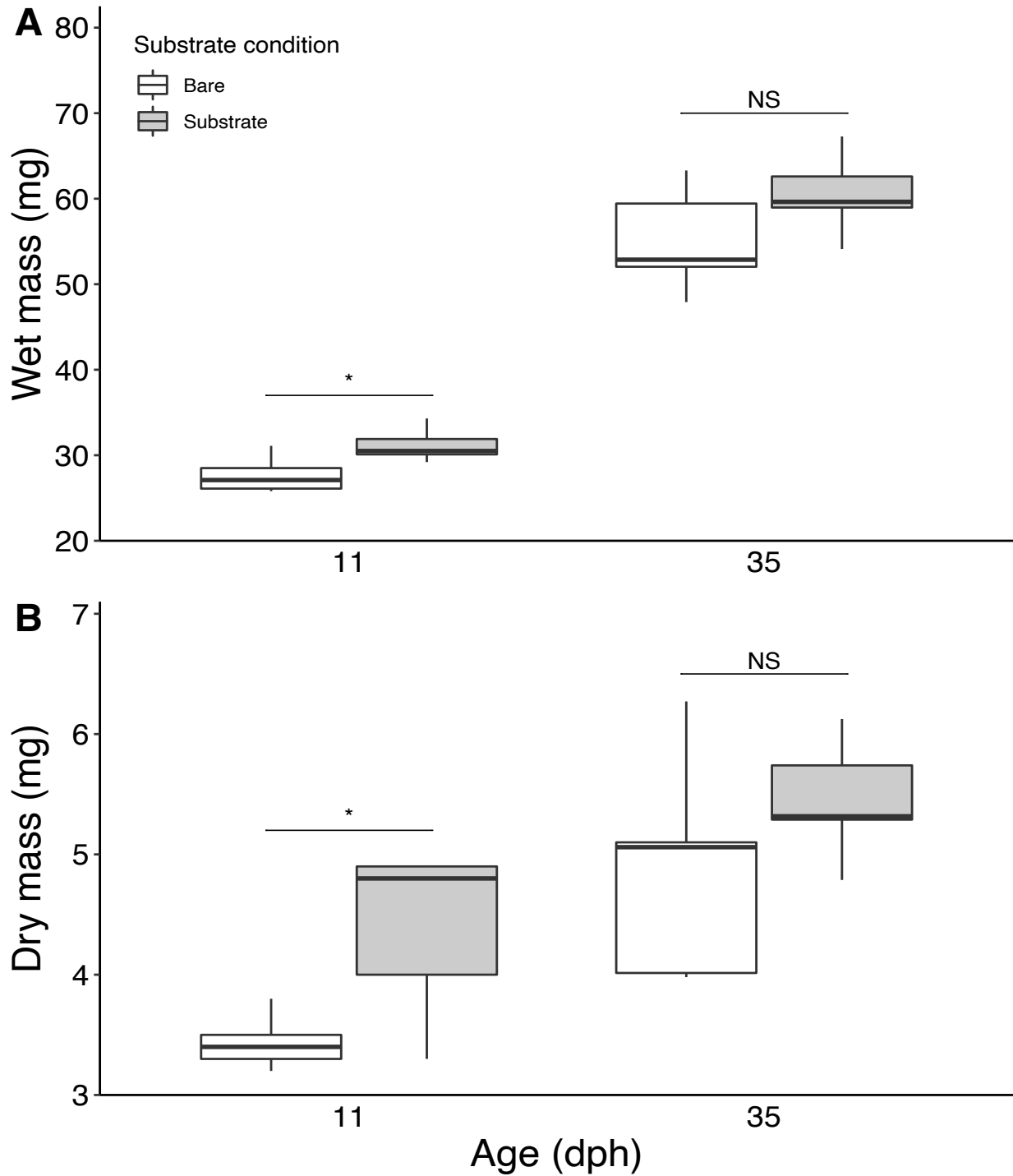


Figure 2.1 A) Wet mass and B) dry mass of larval white sturgeon (*Acipenser transmontanus*) reared with and without substrate at 11 and 35 days post-hatch. The boxplot represents the median and 25th and 75th percentiles. The whiskers represent the smallest and largest values within 1.5 times the inter-quartile range of the percentile boundaries. '*' indicates a statistical significance level of $p < 0.05$. 'NS' indicates the difference is not statistically significant.

Specific growth rates measured by both wet and dry mass were significantly different between larvae reared with and without substrate (Figure 2.2). For specific growth rate measured by wet mass, both substrate and bare treatments gained mass over the study period. Larvae reared with substrate gained 3.22 ± 0.23 %/day and larvae reared without substrate gained 2.81 ± 0.32 %/day ($t_{[8]} = -2.38$, $p = 0.044$, $g = 1.36$). However, specific growth rates measured by dry mass do not follow the same pattern. The larvae reared with substrate gained 0.64 ± 0.27 %/day, whereas the larvae reared in bare tanks lost -0.03 ± 0.54 %/day ($t_{[8]} = -2.471$, $p = 0.038$, $g = 1.41$). The water content of larval tissues was not significantly different at 11 dph and 35 dph. At 11 dph, larvae reared with substrate were 85.93 ± 2.41 % water, compared to 87.52 ± 1.30 % water when reared in bare tanks ($t_{[8]} = -1.30$, $p = 0.23$, $g = 0.74$). The water content of the larvae reared without substrate had a significantly higher variance at 35 dph ($s^2 = 0.011$) than those reared with substrate ($s^2 = 0.00019$; $F_{[4,4]} = 56.25$, $p = 0.0018$). At 35 dph, larvae reared in substrate were 91.20 ± 0.14 % water and larvae reared without substrate were 91.48 ± 1.30 % (Welch $t_{[4.14]} = 0.58$, $p = 0.59$, $g = 0.33$).

The mortality rates of larvae reared with and without substrate were not significantly different. Larvae reared with substrate had a mortality rate of 39.3 ± 7.2 % over the study period, compared to 41.67 ± 7.9 % in the bare treatment ($t_{[7]} = 0.46$, $p = 0.66$, $g = 0.28$).

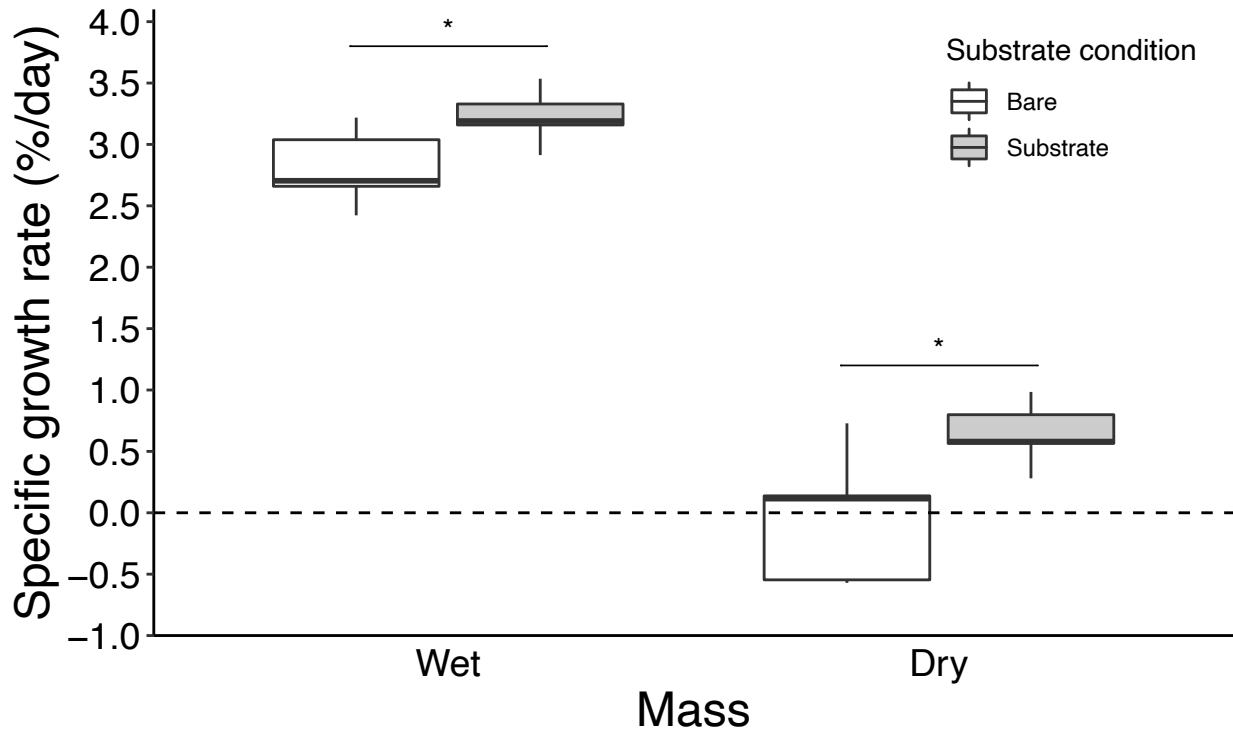


Figure 2.2 Specific growth rates of larval white sturgeon (*Acipenser transmontanus*) reared with and without substrate as measured by wet and dry mass over 35 days post-hatch. The dashed line indicates a growth rate of zero.

2.3.2 Influence of Periods of Starvation on Growth and Larval Condition

Final wet mass was negatively associated with period of starvation at 35 dph ($R^2 = 0.37$, $F_{[1,34]} = 19.64$ on 1,34 DF, $p < 0.0001$; Figure 2.3A). This trend was also observed in the final dry masses ($R^2 = 0.553$, $F_{[1,30]} = 37.11$, $p < 0.0001$; Figure 2.3B). In addition to affecting the total mass of the larvae, the water content of tissues was significantly higher as the duration of starvation increased when measured at 35 dph ($R^2 = 0.42$, $F_{[1,31]} = 21.98$, $p < 0.0001$; Figure 2.4). Duration of starvation also decreased the body condition (K) of larvae ($R^2 = 0.47$, $F_{[1,31]} = 27.85$, $p < 0.0001$; Figure 2.5).

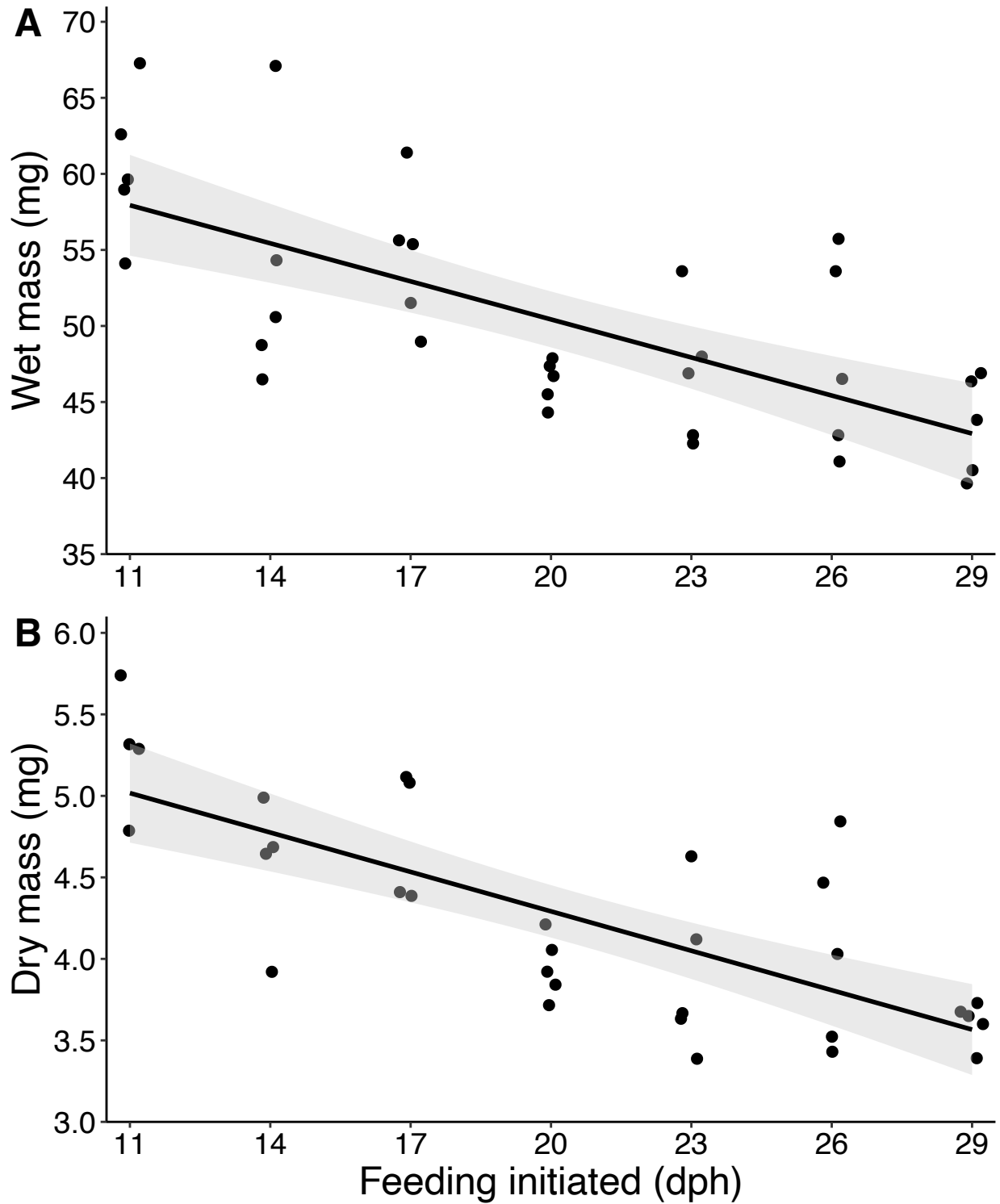


Figure 2.3 A) Wet mass and B) dry mass (mg) of larval white sturgeon (*Acipenser transmontanus*) at the end of the study period (35 days post-hatch; dph). Delayed initiation of feeding was negatively related to final wet mass.

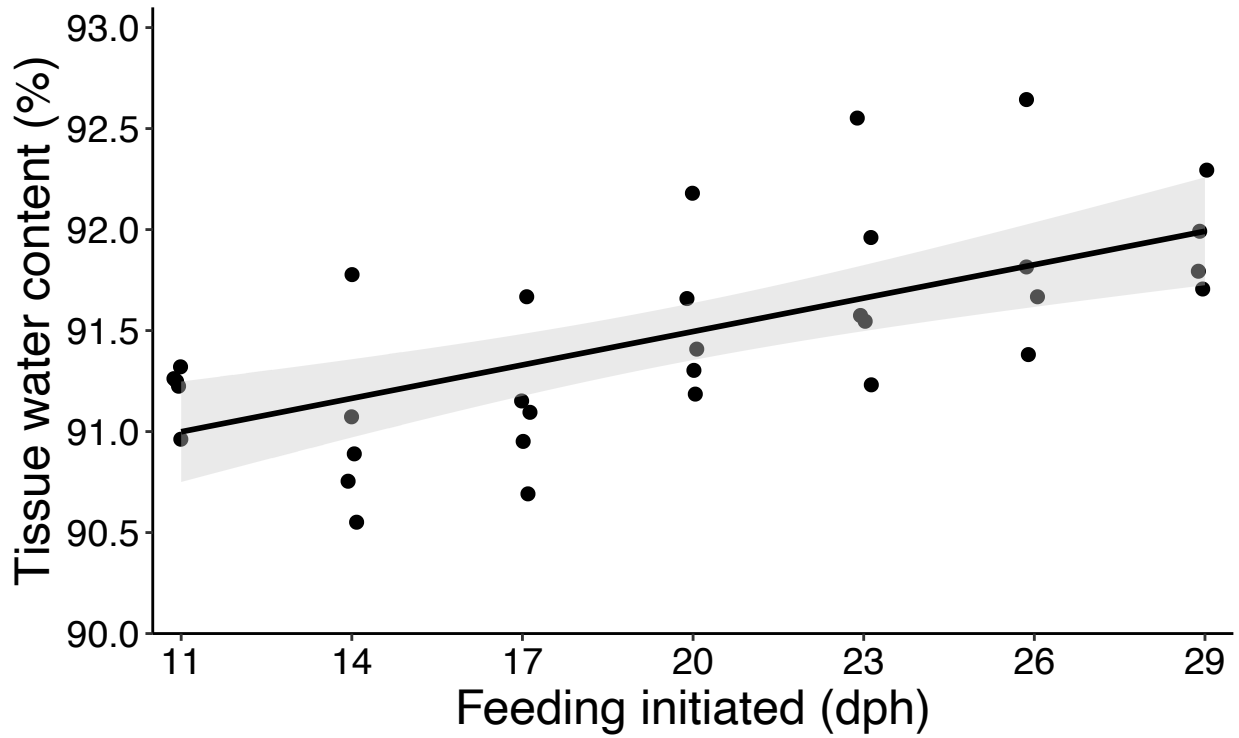


Figure 2.4 Tissue water content (%) of larval white sturgeon (*Acipenser transmontanus*) at the end of the study period (35 days post-hatch; dph). Water content was positively related with day of initiation of feeding.

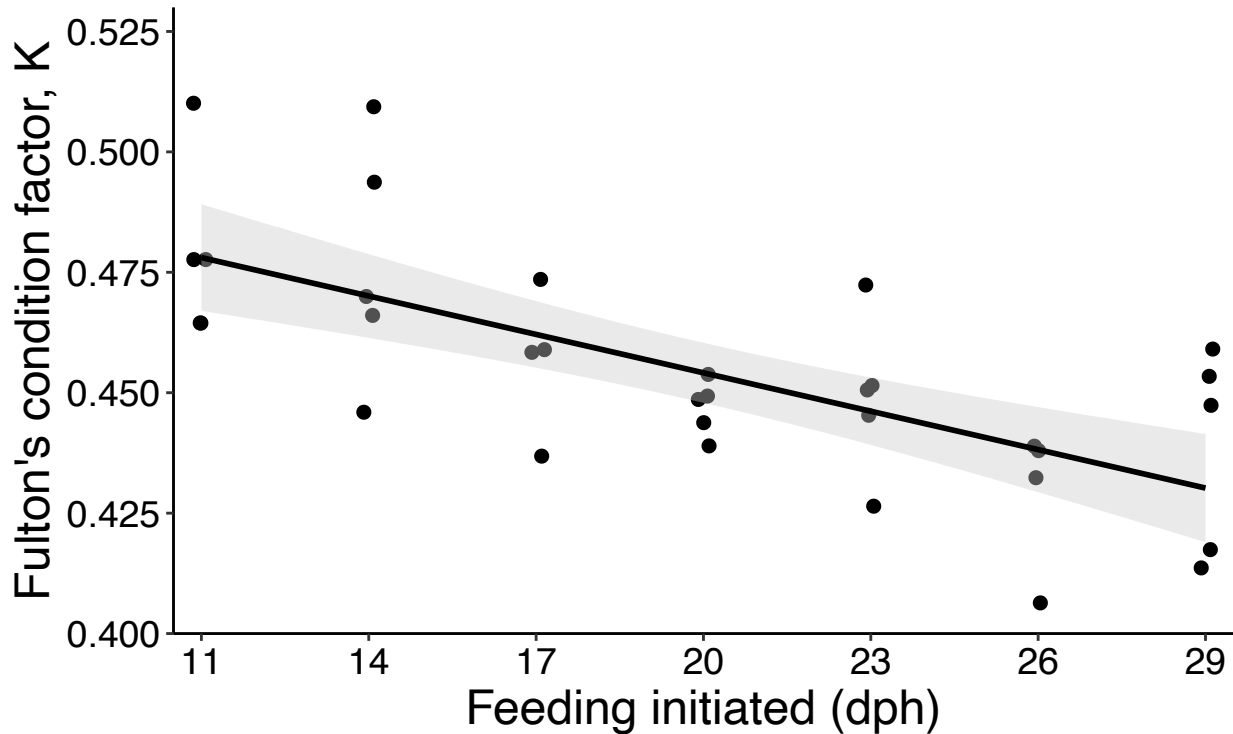


Figure 2.5 Fulton's condition factor, K, of larval white sturgeon (*Acipenser transmontanus*) at the end of the study period (35 days post-hatch; dph). Poor condition was related to increasing days of starvation.

Specific growth rate was lower with longer periods of starvation ($R^2 = 0.34$, $F_{[1,34]} = 17.28$, $p < 0.001$; Figure 2.6A). When measured as wet mass, all treatments gained mass over the study period. Even in the maximum starvation period of two weeks, the 29 dph treatment gained an average of 2.25% body mass/day. Specific growth rate measured by dry mass also declined with increased periods of starvation ($R^2 = 0.64$, $F_{[1,31]} = 56.24$, $p < 0.0001$; Figure 2.6B). Unlike wet mass, some treatments lost dry mass over the study period. The treatments with 9 or more days of starvation before the initiation of feeding (20-29 dph), lost dry mass over the study period. Additionally, the growth trajectories for wet and dry masses had contrasting patterns. Wet masses generally increased from 11 dph to 20 dph, slowing or plateauing growth between 20

and 26 dph and finally increasing to 35 dph for all treatments (Figure 2.7A). In contrast, dry mass increased between 11 dph to a peak at 18-22 dph, subsequently decreasing in mass to 26-32 dph (Figure 2.7B). In all but one treatment (23 dph), mass subsequently increased for the remainder of the study to 35 dph.

Although duration of starvation influenced all performance metrics measured in this study, it did not have a significant effect on the total mortality rate of larvae ($R^2 = 0.016$, $F = 0.5058$, 1,32 DF, $p = 0.48$). Mean mortality rate across all treatments was 42% over the 35-day study period for all treatments.

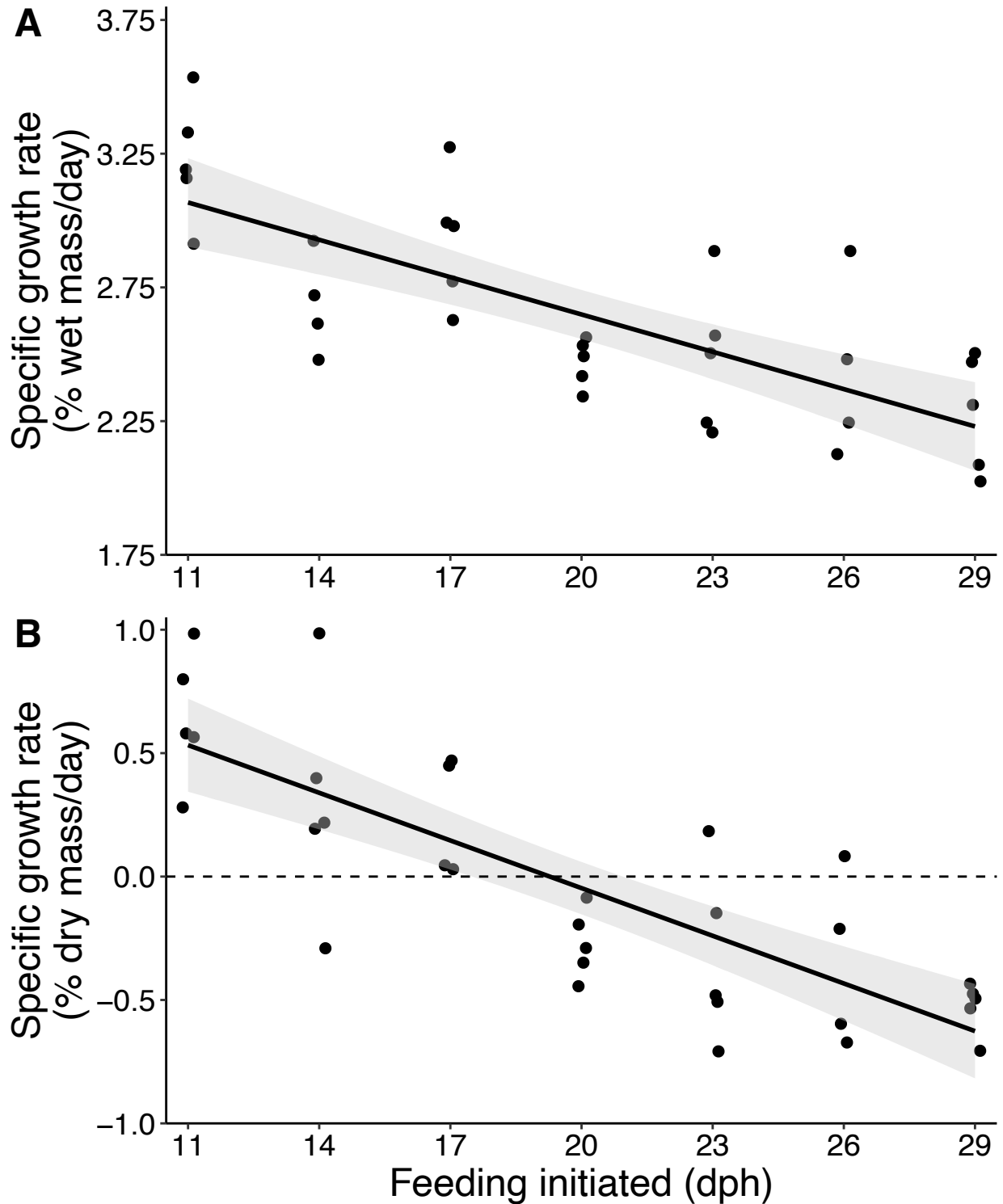


Figure 2.6 Specific growth rates of larval white sturgeon (*Acipenser transmontanus*) that survived to the end of the study period (35 dph) measured by A) wet mass and B) dry mass. The dashed line indicates zero growth over the study period.

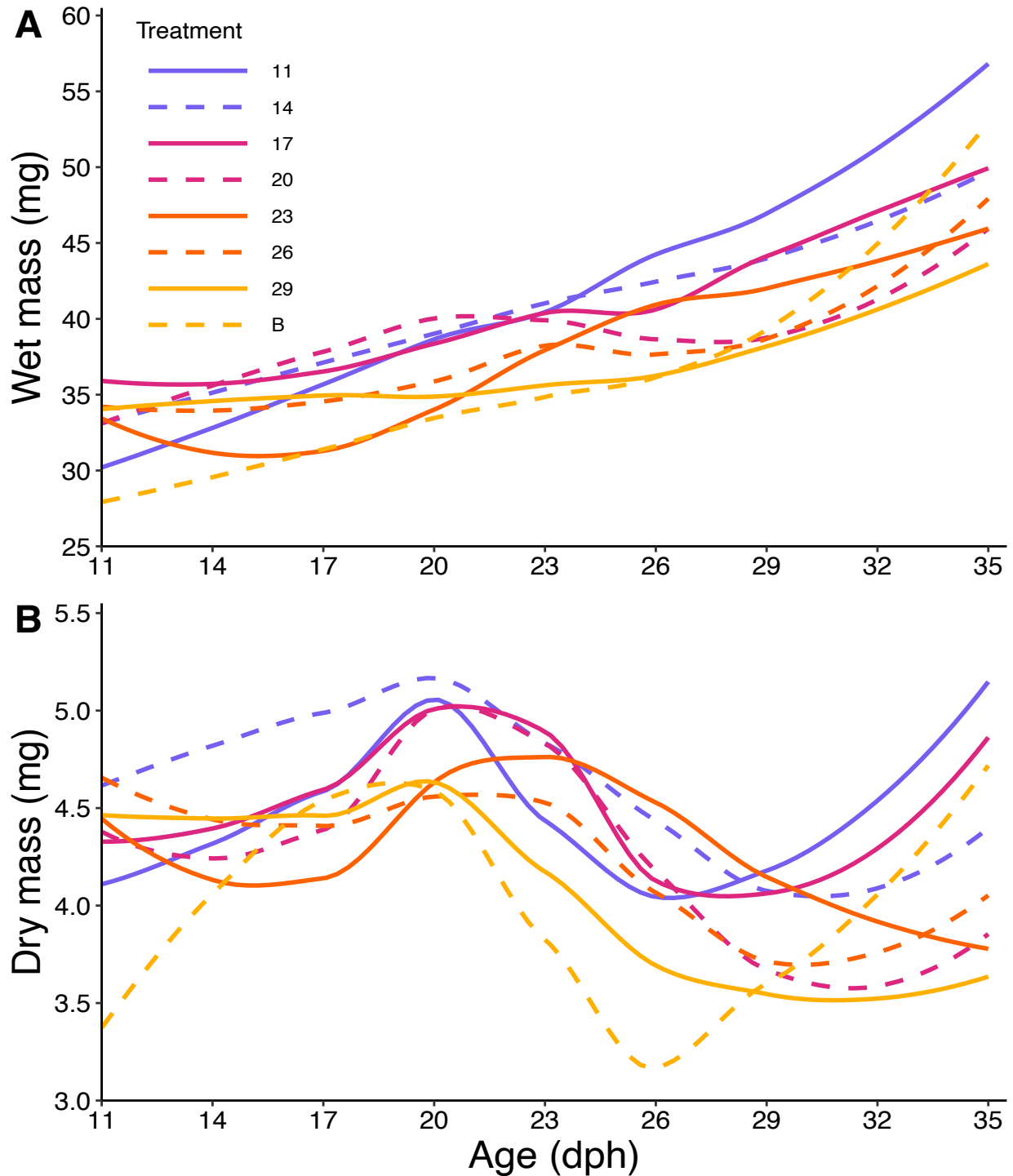


Figure 2.7 Mean growth trajectories of larval white sturgeon (*Acipenser transmontanus*) between 11 and 35 days post-hatch (dph) measured in A) wet mass and B) dry mass. Treatment denotes the day of initiation of feeding, with “B” representing larvae reared without substrate in the yolk sac stage and feeding initiated at 11 dph. A single larva was randomly selected for weighing from each tank in three-day intervals from 11 dph to 35 dph.

2.4 Discussion

Members of the Order Acipenseriformes are among the most endangered freshwater fish in the northern hemisphere (Pikitch et al. 2005). With ongoing recruitment failure in three of six Canadian white sturgeon populations, identifying causes of recruitment failure is essential for planning and implementing effective recovery actions.

Investigating knowledge gaps of the basic biology of white sturgeon during the early life history, including growth and mortality rates, are particularly important to confirm proposed hypotheses of recruitment failure (Fisheries and Oceans Canada 2014).

Annual spawning behaviour is intact in most population segments and viable eggs have been recovered and successfully reared for laboratory studies and conservation aquaculture, supporting the assertion that the main bottleneck to recruitment is survival in the YSL to early juvenile (Age-0) stages (Hildebrand et al. 2016). Egg survival is also variable, primarily affected by sedimentation and predation (Brannon et al. 1985; Kock et al. 2006). As studying these stages in the wild is currently difficult due to the limited success beyond the egg stage, laboratory studies can act as important starting points for knowledge generation.

2.4.1 Substrate Improved Growth in Larval White Sturgeon

Insufficient interstitial hiding spaces in substrate during the YSL stage has been hypothesized to contribute to recruitment failure in the wild, but the mechanisms of why hiding is beneficial continues to be tested. I found that the presence of substrate contributed to better growth outcomes during the larval stages of white sturgeon. At 11 dph, approximately the time of transition to exogenous feeding and the start of the FL

stage, larvae that were reared in substrate were heavier when measured by both wet and dry mass. At 35 dph, the final mass measurements were not significantly different between substrate and bare treatments for both wet and dry mass, but larvae reared in substrate were approximately 10% heavier. Condition factor and water content of larvae at 11 dph and 35 dph were not significantly different between substrate treatments. This pattern may suggest that FL may be able to exhibit compensatory growth with *ad libitum* feeding opportunities and overcome the disadvantage of lacking interstitial spaces in the YSL stage. Yet, the growth rates measured in this study do not fully support this hypothesis. The SGR for the duration of the study was higher in larvae that were reared in substrate as measured by wet and dry mass. If compensatory growth enabled FL to grow rapidly and completely overcome the disadvantage of rearing without substrate during the YSL period, growth rates over the study period would be similar between substrate and bare treatments. Varying magnitudes of compensatory growth after a period of starvation has been found in the FL and early juvenile stages of Chinese (*Acipenser sinensis*), green (*Acipenser medirostris*), shortnose (*Acipenser brevirostrum*), and stellate (*Acipenser stellatus*) sturgeon (Hardy 2000; Liu et al. 2011; Poletto et al. 2018; Florescu (Gune) et al. 2019). If the allocation of yolk energy to swimming in the bare treatments during the YSL stage may approximate short-term starvation in the FL stage, sturgeon larvae may be able to recover to some extent with sufficient food availability at the initiation of feeding. Finally, condition factor was lower at 35 dph than 11 dph but rather than being a true decline, it is likely that ontogenetic changes in morphology from early in larval development to metamorphosis to the juvenile stage are occurring. For example, elongation of the tail and rostrum during this

period has been found in Siberian (*Acipenser baeri*) and green sturgeon (Gisbert 1999; Gisbert and Doroshov 2006).

Evidence for the beneficial effects of the presence of substrate during the YSL stage has previously been found for white sturgeon. Larvae reared without substrate during the YSL stage have been found to absorb their yolks slower and exhibit delays in gut development (Baker et al. 2014). In contrast, Boucher et al. (2014) found that white sturgeon YSL reared in substrate or bare tanks had the same rate of yolk absorption, yet YSL reared in substrate were significantly heavier at the end of the stage. YSL reared without substrate apparently spent more of their limited energy reserves on swimming rather than growth and development. In a follow up study, Boucher et al. (2018) found that YSL and FL reared without substrate had lower aerobic scope and lower whole-body glycogen concentrations than those that were reared with substrate. Rearing without substrate could therefore impair larvae's ability to swim to escape predation and forage for food. While these factors may not be as relevant to the hatchery environment, the carryover effects into later life history stages are unknown and could disadvantage juveniles upon release into the wild. In contrast to my result of similar survival rates between larvae reared in substrate and in bare tanks, Boucher et al. (2014) found 20% higher survival when larvae were reared in gravel versus bare tanks (85% and 67%, respectively). The reason for the discrepancy between our results is unclear, as they were fed similar diets and the larval density per volume was lower than in my study. However, maternal influence on offspring development leading to variability in survival has been previously suggested (Bates et al. 2014). The presence

of coarse gravel substrate during the yolk sac larval stage is also beneficial for Atlantic sturgeon (*Acipenser oxyrinchus*) during their hiding phase. Larvae reared in gravel had higher dry mass and energy content (Gessner et al. 2009). In summary, this evidence, though limited to a few studies, suggests that interstitial hiding space in substrate is important for successful growth, development and survival of white sturgeon larvae and further studies to investigate the extent of these patterns are warranted.

Despite evidence that the presence of substrate during the YSL stage of white sturgeon is beneficial, the use of substrate in artificial propagation of fish is not widespread. The use of bare tanks to facilitate waste removal and prevent disease, particularly in the early life history, is common practice for fish culture (George et al. 2009). However, using artificial substrates for the short YSL period where larvae are not feeding and are producing little solid waste is low risk for disease and has lasting benefits for the growth and survival outcomes of larval and juvenile sturgeon (Boucher et al. 2018). Larvae reared in artificial substrate, i.e. 'bio-balls', had comparable outcomes to those reared in gravel, with the additional benefits of artificial substrate being lighter, providing more hiding space per volume of substrate, and can be sterilized for disease prevention. These materials were used successfully as artificial substrate in my study and by Boucher et al. (2018). Therefore, evidence supports the use of artificial substrate for laboratory propagation of sturgeon to improve larval outcomes, and the practice has been recommended for aquaculture (Chebanov and Galich 2011). Larvae reared without substrate show significantly higher levels of whole body cortisol, indicating elevated stress levels (Bates et al. 2014). Using larvae that have been propagated

without substrate to study the growth and behaviour of the early life history stages of sturgeon may unintentionally bias results by using larvae that are smaller, slower and experiencing higher stress than their potential. Adopting the practice of rearing YSL in artificial substrate can also provide effective, low cost enhancement of larvae propagated in conservation hatcheries, that are often limited by funding (Brown and Day 2002).

2.4.2 Starvation Decreased Growth and Health Metrics of Feeding Larvae

Starvation has been considered one of the most important regulators of larval fish survival, but the extent of its control of overall recruitment rate has been debated (Leggett 1986; Leggett and Deblois 1994). In my study, periods of starvation between the exhaustion of endogenous yolk stores and initiation of exogenous feeding influenced all measures of growth and health. Condition factor, specific growth rate, and mass at the end of the study period were all negatively related with increasing periods of starvation. Even a relatively short period of starvation affected the growth of FL. The larvae in the treatment group with the lowest interval of starvation (3 days, initiating feeding at 14 dph) were smaller and grew slower than the larvae that began feeding at the exhaustion of the yolk sac (11 dph). Periods of compensatory growth after starvation have been observed in juvenile cyprinids and salmonids (Wieser et al. 1992; Ali et al. 2003). I did not observe compensatory growth in my study, and if it was occurring, I would expect to see a temporary increase in growth rate after the initiation of feeding. This pattern was not apparent in the wet and dry mass trajectories.

Patterns of growth rates and mass trajectories differed between measurements of wet mass and dry mass. When measured by wet mass, all treatments gained mass over the study period, but treatments that began feeding at 20 dph (9 days of starvation) or later lost dry mass. When larvae are experiencing severe nutritional stress, protein and lipid in tissues are broken down to resist starving to death. When these compounds are metabolized, the space they occupied in the tissues fill with water (Hung et al. 1997). This results in apparent increasing wet mass, when the larvae are in fact wasting away and losing their fat stores and muscle tissues. Adopting dry mass as a metric of health for larval sturgeon is therefore critical to accurately assess the nutritional status of larvae that may be starving. Though this measurement method is lethal, it could easily be used in conjunction with the gut dissection sampling methods currently in use for assessing starvation in larval white sturgeon in the Columbia River (For example Howell and McLellan 2006, 2007). Interestingly, all groups experienced a sharp decline in dry mass between approximately 20 and 26 dph. Larvae experience rapid development as they near metamorphosis and the energetic demands in this period may be too high; depletion of lipid stores could be required to supplement the energy gained by feeding (Boucher et al. 2014).

Although periods of starvation reduced all health metrics measured in this study, the larvae were resistant to starvation-associated mortality. Mortality rates were similar across all treatment levels. White sturgeon have been found to accumulate lipid reserves in their liver and intestines during the YSL and FL stages, allowing them to endure periods of food deprivation without dying (Gawlicka et al. 2002; Boucher et al.

2014). These reserves have also been found in Siberian and green sturgeon larvae (Gisbert and Williot 2002; Gisbert and Doroshov 2003). Although periods of starvation did not directly elevate mortality in my study, starvation in larval sturgeon has been associated with factors that could reduce overall survival. In green sturgeon, larvae that were deprived of food exhibited deterioration of gut tissues after 5 days of starvation, increasing to necrosis after 10 days (Gisbert and Doroshov 2003). Low feeding rates also led to decreased liver heat-shock proteins and thermal stress resistance in larval white sturgeon (Deng et al. 2009).

2.4.3 Evidence for the Point of No Return

Blaxter and Hempel (1963) characterized the point of no return as a tipping point where larvae can no longer endure starvation despite food availability, and mortality rates rapidly increase over the following days. By the above definition PNR was not reached in my study, and all starvation treatment groups gained wet mass after the initiation of feeding, and all but one group (23 dph) gained dry mass. Total mortality rates across my treatments were similar (42%), and no sharp increase in mortality over time was observed. Larvae showed a high resistance to starvation, with the longest starvation treatment of 18 days (29 dph) having mortality rates equal to those that were fed immediately at the point of yolk exhaustion (11 dph). Similarly, Gisbert and Williot (1997) found 17 dph Siberian sturgeon were able to eat and gain wet mass after 12 days of starvation at 18 °C. Although the larvae were able to recover after initiation of feeding, mortality rates were elevated during the starvation period resulting in approximately 40% of the larvae surviving to the point of initiation of feeding at 17 dph.

The period before reaching the PNR is long in other species of sturgeon. Hardy (2000) found that shortnose sturgeon could start feeding up to 18 days (33 dph at 17 °C) of starvation after the exhaustion of the yolk before reaching the PNR, but survival to this period was low (42%). Russian sturgeon (*Acipenser gueldenstaedtii*) larvae were able to feed up to the PNR at 22 dph, with only 20% of larvae surviving to the initiation of feeding (Zhang et al. 2009). Of the few studies published testing the PNR for sturgeon larvae, only one identified a short critical period. For Chinese sturgeon, larvae reached the PNR after 4 days of starvation (15 dph) subsequent to yolk exhaustion (Chai et al. 2011). The reason for this finding is unclear, but perhaps the larvae reached PNR faster when reared at aquaculture temperature (23 °C), rather than a lower temperature the larvae would experience in the wild (Zhang et al. 2019).

Patterns of mortality for larval sturgeons do not support the classical definitions of the point of no return (Blaxter and Hempel 1963). The original definition of the PNR is the time at which more than half of starving larvae cannot feed when offered food, after which mortality sharply increases. The mortality evidence reviewed above suggests a large proportion of starving sturgeon larvae die before reaching this definition of PNR. Using Hardy's (2000) results as an example, he found that 56% of shortnose sturgeon larvae offered food after 18 days of starvation were able to consume it. Survival to this first feeding date was only 42%, and overall survival to the end of the experiment was 29%. The majority of the mortality happened before the PNR, not after. This pattern was also found by Gisbert and Williot (1997) and Zhang et al. (2009). Therefore, PNR may not be a useful metric of starvation resistance for sturgeon and other fishes with large

yolks. This definition of PNR likely represents the final opportunity to feed for the most resilient larvae of a cohort, but it is a threshold that most starving larvae will not reach.

2.4.4 Evidence of Larval Starvation in the Wild and its Contribution to Recruitment Failure

Limited food availability for the FL stage has long been a hypothesized driver of recruitment failure in white sturgeon populations, but evidence to support this hypothesis is limited (Brannon et al. 1985; Parsley et al. 1992; Howell and McLellan 2006, 2007). Much of the historical floodplain habitat that larvae would have access to during periods of high flows and flooding has been disconnected from the mainstem river through the armouring of shorelines and decreased water levels due to flow modification by dams (Coutant 2004). This seasonal pulse of invertebrates from the flooding of riparian areas is an important food resource for riverine fishes that has largely been attenuated by flow modification (Junk et al. 1989; Baxter et al. 2005). Decreasing productivity of aquatic invertebrates downstream of dams as a result of nutrient retention in upstream reservoirs is also a concern for prey availability for larval and early juvenile sturgeon, and (McAdam 2012; Reihart 2016).

The habitat “match-mismatch” hypothesis states that dispersing larvae must arrive at their foraging habitat at the time their prey are available, otherwise the cohort may experience recruitment failure (Cushing 1974, 1990). This hypothesis is an extension of the critical period hypothesis, highlighting the importance of spatial and temporal synchronicity between predator and prey emergence during the critical period for

feeding (Houde 2008). Sampling efforts to establish if white sturgeon FL are experiencing food limitation and starvation in the wild at their settlement sites has yielded inconclusive results. In the upper Columbia River, the majority of the larvae captured had not exhausted their yolks (Howell and McLellan 2006, 2007). The oldest larvae caught in yearly sampling efforts in Lake Roosevelt are 15 dph (Hildebrand and Parsley 2013). Of the few that had exhausted their yolks, 77-100% have empty stomachs. Similarly, 98.8% of larvae collected by Reihart (2016) had not completely exhausted their yolk sac. Of the 1.18% that had exhausted their yolk, 58% had no prey items in their stomachs. While finding larvae with empty stomachs is concerning, my results suggest that inferences cannot be made about the outcome of food deprivation at this age because the larvae are too young. If sampling efforts are shifted later in the year or further from known spawning locations, larvae may be old enough to yield results that could determine if larvae are starving in the upper Columbia. In the lower Columbia, Muir et al. (2000) found no evidence of starvation in FL upstream or downstream of the Bonneville Dam. Of the 203 larvae sampled downstream, 2.5% had empty stomachs, and of the 149 sampled in the reservoir, 0.7% had empty stomachs. While more larvae below the dam had empty stomachs, I would expect to see a larger proportion of larvae affected if nutrients were being retained in the reservoir and affecting productivity so severely as to cause starvation. Starvation resistance in larval fish drastically increases if a larva has successfully begun to feed exogenously before a period of starvation (Blaxter 1969). Although invertebrate productivity has been hypothesized to be limiting for larval sturgeon, the chance that they find no suitable prey items is low because they eat a wide variety of prey species (Muir et al. 2000; Reihart

2016; Hindle 2018). Further, in a laboratory study of white sturgeon foraging behaviour, larvae that did not encounter food at their initial settlement site were observed to re-enter the drift (Brannon et al. 1985). If a drifting larva settles in a patch completely devoid of suitable prey in the wild, it would likely leave the patch to forage elsewhere. This raises the critical point of whether such larvae might increase their risk of predation mortality as a consequence of continued food searching.

Animals that undergo ontogenetic habitat shifts are faced with a trade-off between maximizing growth rates and minimizing predation risk (Werner and Gilliam 1984; Werner and Anholt 1993). The shift from interstitial spaces at spawning habitat to the juvenile rearing locations downstream by drifting represents an enormous risk for larvae but may be beneficial to locate higher feeding opportunities and lower intraspecific competition with their cohort; starving larvae may be exposed to more predation and take higher risks to feed (Parsley et al. 2002). As duration of drift has been suggested to be a long, potentially multi-day journey, white sturgeon larvae may drift before 100% of their yolk is absorbed (McCabe and Tracy 1994; Kynard and Parker 2005). If larvae do not begin to feed in their interstitial hiding spaces for a mixed feeding period before they initiate drift, it may be advantageous to reserve some yolk provisions for energy to actively swim downstream rather than use all reserves for growth before drift (Kynard and Parker 2005). Alternatively, drifting with yolk reserves may indicate that some factor(s) at or near spawning beds is unsuitable and larvae take the risk to drift to escape poor conditions. Mainstem dams have altered the geomorphological sediment regimes of rivers that white sturgeon occupy, leading to the infilling of historical

spawning coarse substrates with fine sediments and reducing or eliminating hiding spaces (Blair and McPherson 1999; Paragamian et al. 2001; McAdam et al. 2005; McAdam 2015). Laboratory and field studies have yielded evidence that larvae that do not have access to substrates with sufficient interstitial habitat drift earlier, are poorer quality and have elevated predation risk (Brannon et al. 1984; McAdam et al. 2005; McAdam 2011, 2015; Crossman and Hildebrand 2014). Consequently, these shifts may be a larger contributor to ongoing recruitment failure than larval starvation. Studies that investigate substrate condition, yolk absorption and feeding status, and drift timing are therefore crucial to understanding if environmental deficiencies leading to recruitment failure are acting at the upstream spawning habitat, or downstream feeding habitat.

Chapter 3: Growth and Intraspecific Competition of Age-0 White

Sturgeon

3.1 Introduction

White sturgeon is the largest freshwater fish in North America and is indigenous to three large river systems in western North America: the Fraser, Columbia and Sacramento-San Joaquin river basins (Ptolemy and Vennesland 2003; Hildebrand et al. 2016). White sturgeon populations in Canada are at risk of extirpation, with four of the six populations federally listed as endangered under the Species at Risk Act since 2003 (Fisheries and Oceans Canada 2014). Despite growing interest by the scientific community, recovery efforts for white sturgeon populations have had mixed success and knowledge gaps of basic biological information for white sturgeon persist (Hildebrand et al. 2016). In populations with low recruitment, recovery strategies have prioritized conservation aquaculture in an attempt to increase the abundance of juvenile fish (for example Dinsmore et al. 2015; Robichaud and Gingerich 2015). Growth and survival of juveniles released from these programs has been variable, and more research is needed to assess the success of hatchery fish post-release. With little to no recruitment over the past four decades in several populations, it is critical to understand the ecology of juvenile sturgeon. Because of this ongoing recruitment failure, opportunities to study the ecology of young white sturgeon in situ have been diminished. Recruitment failure has been associated with flow modification by dams but the mechanisms remain unconfirmed because the drivers appear to affect the life history stages that are difficult to observe in the wild: between egg release at spawning sites to yearlings under 20 cm

in length (COSEWIC 2012). Of particular interest, growth and mortality rates in the early life history stages of white sturgeon, beyond those derived from aquaculture practices, have been understudied.

Growth rates of white sturgeon have been thoroughly investigated in the aquaculture literature. Manipulations of food ration, feeding frequency and temperature conditions have been tested to maximize growth and reduce costs of feed (Cui et al. 1997; De Riu et al. 2012; Rodgers et al. 2018). Because of their late maturation and highly valuable caviar, research efforts have focused on growing fish as rapidly as possible. These studies are important baselines for growth under ideal conditions and can be used to compare to indices of growth in the wild (Elliott and Hurley 1995). However, performance in aquaculture environments often exceeds growth that could be achieved under natural conditions. In aquaculture, juvenile sturgeon are frequently sorted into homogenous size groups through a process called “grading” to simplify feed regimens and maximize growth (Chebanov and Galich 2011). This process reduces intraspecific interactions and is beneficial for increasing yield for aquaculture products. However, this minimization of variation between individuals impacts our ability to extend the results of aquaculture studies to predict how individuals may interact and grow under natural conditions (Doyle and Talbot 1986; Bjornson and Anderson 2018). Therefore, little is known about intraspecific interactions in the early life history of sturgeon and their implications for growth and mortality rates due to competition for limited resources.

Interference competition for food occurs when one individual feeds at a high rate, thereby lowering the available resources and decreasing feeding rates of others (Ward et al. 2006). This unequal distribution of resources has consequences for individual growth and mortality rates (Metcalf 1986; Holm et al. 1990; Nunn et al. 2012).

Subordinate fish may suffer from being outcompeted in scramble competition, where faster and more efficient individuals consume a disproportionate amount of the available resources, or be actively excluded from feeding areas by aggressive competitors in contest competition (Łomnicki 2009). Fast growth rates in early life history are favourable for increasing overwintering survival (when resources are scarce and metabolic rates are lower), reaching a size refuge from predation, and meeting the energetic demands of migration (Arendt 1997). Selection for these traits in the early life history can result in fitness advantages for the adult stages, including earlier sexual maturation and higher fecundity (Werner and Gilliam 1984).

The objective of my study was to investigate the role that intraspecific competition plays in influencing growth and mortality rates in age-0 juvenile white sturgeon. I tested the hypothesis that reduced food ration and high conspecific density will increase intraspecific competition between juvenile white sturgeon, leading to poor growth and survival outcomes. To test this hypothesis, I performed a laboratory experiment where I reared 12-week-old juvenile white sturgeon for four weeks at four densities and two ration levels. I predicted that the treatment with the highest density and lowest ration would have the lowest mean growth rate and highest mean mortality rate.

3.2 Methods

3.2.1 Broodstock

The white sturgeon used in this study were acquired from the Nechako White Sturgeon Conservation Centre in Vanderhoof, British Columbia. Wild adult white sturgeon were captured for broodstock from the Nechako River in May 2019. Ovulation of female fish was induced on June 3rd, 2019 using a luteinizing hormone-releasing hormone analogue (Syndel Laboratories Ltd., Nanaimo, British Columbia). Eggs were collected from three females and fertilized with a mixture of milt collected from eight male fish, resulting in the three maternal families used in this study. The larvae hatched on June 13th, 2019 and were reared to the juvenile life history stage (beginning at approximately 40 days post-hatch, dph) at the hatchery. The juveniles were transported in coolers by air freight to the Vancouver campus of the University of British Columbia on August 14th, 2019 (62 dph).

3.2.2 Husbandry

After transportation, the juvenile sturgeon were transferred into an acclimation tank at 14 °C water temperature in the InSEAS facility in the Department of Zoology. Juveniles from the three families were mixed in a single holding tank. The circular tank was 1.0 m in diameter and 1.0 m deep, with constant radial flow (approximately 10 cm s⁻¹) from a recirculating system. The fish were fed EWOS[®] Micro (Cargill, Minneapolis, Minnesota) 1.2 mm pellets three times per day *ad libitum*. Any remaining food that was not eaten was removed daily with an aquarium siphon. After two weeks of acclimation, fish were randomly selected for the experiment.

The experiment was conducted in an environment chamber set to maintain an air temperature at 14 °C and a 14L:10D photoperiod. Twenty-four, 40 L standard glass aquarium tanks (50 cm x 25 cm x 50 cm) were wrapped with black plastic to reduce ambient light and prevent the fish from seeing into adjacent tanks. The aquaria bottoms were covered with 200 ml of fine, multicolour gravel (round, approximately 5 mm diameter) and three 75-mm long pieces of 63.5-mm diameter white PVC pipe were added to each aquarium for substrate complexity and hiding spaces. The tanks were filled with dechlorinated municipal water acclimated to ambient temperature inside the chamber (13.5 °C water temperature, 7 pH, 0 ppm ammonia). Water quality was maintained in the tank using a charcoal and foam media filter. Water was passed through the filter using lift from an air stone, simultaneously oxygenating the water. Fish waste was removed from the tank by siphoning and replacing two thirds of the tank water daily. pH and ammonia values were checked every other day with API® pH and ammonia test solutions (Mars Fishcare North America Inc., Chafont, Pennsylvania).

3.2.3 Experiment Design

Tanks were randomly assigned one of eight treatments: densities of 1, 3, 5 or 7 fish/tank on a full or half ration feeding schedule. Each individual was randomly assigned to a tank. To track the identities of individuals over the course of the study, fish were given a visible mark. To apply the mark, fish were anesthetized by immersion in a bath of 75 mg L⁻¹ tricaine methanesulfonate (Finquel MS-222, Argent Laboratories, Redmond, WA) buffered with 150 mg L⁻¹ sodium bicarbonate for five minutes. Two

marks of acrylic craft paint (Liquitex® Basics™, Cincinnati, Ohio) diluted 1:3 with dechlorinated municipal water were injected subdermally with 31-gauge syringe on the ventral surface adjacent to the scutes (Lotrich and Meredith 1974). Combination and location of two marks of either fluorescent red, blue or yellow were used to create 7 unique codes and were used to track the ID of the individuals within a tank over the study period. Codes were reused across tanks.

The full food ration per tank was determined by multiplying the mean mass of the fish in the tank by the number of individuals and the optimal feeding rate (See Section 1.2.4). The half ration treatments received 50% of the food calculated by the optimal feeding rate. The daily ration was divided into three meals and distributed equally throughout the tank at each feeding. Each meal was rapidly eaten within the first few minutes after feeding, with no excess food remaining. The mass of the fish was measured weekly over the four weeks of this study to calculate growth over each interval. Fish were removed from the tank into a holding container and identified by their visual mark with the aid of an ultraviolet flashlight. Once identified, fish were blotted to remove excess water, weighed (g) and measured for length (mm), then returned to the experimental tank. The new mass measurements were then used to adjust the tank ration for the following week. Rations were also adjusted in the instance of a mortality in a tank to prevent overfeeding of the remaining individuals. At the end of the study, fish were euthanized by immersion in a bath of 250 mg L⁻¹ tricaine methanesulfonate buffered with 500 mg L⁻¹ sodium bicarbonate until 10 minutes past the cessation of opercular movement.

3.2.4 Calculation of Optimal Feeding Rate

The full ration was defined as the optimal feed rate (OFR), where increasing the amount of food will not provide an additional increase in growth. To determine which OFR model to use in this study, I compared three methods. The first model (Equation 3.1) was derived in a study by Cui and Hung (1995) for white sturgeon ranging from 50 to 1,000 g under temperature conditions between 10 and 26 °C:

$$\log_e OFR = -2.88 - 0.25 \log_e W + 0.400T - 0.0077T^2 \quad (3.1)$$

Where the OFR (% body mass/day) is determined by the fish mass in grams (W) and the water temperature in Celsius (T). A more recent OFR model derived by Lee et al. (2014; Equation 3.2) was optimized for white sturgeon between 0.05 g and 800 g, formulated from data of fish reared under temperature conditions of 18 to 23 °C.

$$OFR = 0.00344 e^{-5684 \ln(\sqrt{W})} + 8.695 e^{-0.549 \ln(\sqrt{W})} \quad (3.2)$$

Rodgers et al. (2018) created a correction factor for Lee et al.'s (2014) model for use in their experiment at 11°C. They calculated the percent difference between an OFR calculated by Cui and Hung's (1995) model at 18 °C and 11 °C (71%) and applied it to Lee et al.'s (2014) model. Using this method, I calculated the percent difference between the Cui and Hung (1995) OFR model at 18 °C and 13.5 °C (51%) and applied it as a correction factor to Lee et al.'s (2014) model (Equation 3.3).

$$OFR = (0.00344 e^{-5684 \ln(\sqrt{W})} + 8.695 e^{-0.549 \ln(\sqrt{W})}) * 0.49 \quad (3.3)$$

I compared the three OFR models for the range of initial masses (1.785 – 5.687 g) of the fish used in this experiment (Table 3.1). I selected Cui and Hung's (1995) model of OFR for use in this experiment because it was the lowest option to prevent feeding all treatments at a rate higher than the true OFR.

Table 3.1 Comparison of three optimum feeding rate (OFR, % body mass/day) models for the mean and range of initial masses of juvenile white sturgeon used in this experiment (1.785-5.687 g).

Model	Equation	Temperature (°C)	Mean OFR (%W/Day)	OFR Range (%W/Day)
Cui and Hung 1995	1	13.5	2.291	1.978-2.642
Lee et al. 2014	2	18 - 23	6.342	5.395-7.417
Rodgers et al. 2018	3	13.5	3.123	2.656-3.651

3.2.5 Statistics

Statistical analyses were conducted in the R programming language (version 3.6.1) in the RStudio environment (version 1.2.5019; R Core Team 2019; RStudio Team 2019). Data are expressed as mean ± standard deviation. Linear mixed effects models were fit with restricted maximum likelihood estimation in the *nlme* package (Pinheiro et al. 2020). Type-III sum of squares ANOVA tables with Wald chi-square test statistics were generated for the fixed effects using the *car* package (Fox and Weisberg 2019). The marginal R^2 for the fixed effects of each mixed effects model were calculated using the Nakagawa and Schielzeth method (2013) in the *r2glmm* package (Jaeger 2017).

The first index of growth calculated was the specific growth rate (SGR) (Equation 4; Lugert et al. 2016).

$$SGR = \frac{\ln(w_t) - \ln(w_i)}{t} * 100 \quad (4)$$

Where the SGR (%/day) is determined by the difference between the natural logarithm of the final mass (w_t) and the initial mass (w_i) in grams over time (t , in days). SGR was modelled with a linear mixed effects model for all fish over the first week of the experiment, where the SGR in the first week (SGR_1) is predicted by the density of fish in the tank and ration provided, their interaction and the survival outcome (mortality or survival) of the fish during the experiment. Tank is fitted as a random slope for all mixed effects models in this study to control for non-independence of fish within a tank. The SGR of the fish that survived for the whole 4-week duration was also modelled with a linear mixed effects model using the final mass measurement at the end of the experiment, where the SGR of the surviving fish over the 4-week duration of the experiment (SGR_s) is predicted by the density of fish in the tank and ration provided, and their interaction.

The second metric of growth calculated was the growth efficiency, a metric of the efficiency with which fish convert ingested food into body mass. Growth efficiency was calculated using Equation 5.

$$GE = \frac{\sum w_m - w_i}{f} \quad (5)$$

Where tank growth efficiency (GE) is determined by the sum of the mass gained by all fish in the tank (the maximum mass, w_m , minus the initial mass, w_i), divided by the sum of the amount of food provided to the tank over the study period, f . The GE was calculated on a per-tank basis, as the proportion of the food eaten by each individual fish is unknown. A linear model was fit for GE, where GE was predicted by the density of fish in the tank, the ration provided, and their interaction.

A linear model was also fit for the mortality rate per tank over the entire study period, predicted by the density of fish in the tank, the ration provided, and their interaction. Finally, linear mixed effects models were fit for the final masses of the survivors and mortalities. The mass at the end of the experiment for the surviving fish was predicted by the density of fish in the tank, the ration provided, and their interaction and the initial mass of the fish. The mass at death of those that died was predicted by the density of fish in the tank, the ration provided, and their interaction, the initial mass of the fish, and the number of days the fish survived.

3.3 Results

During the first week of the experiment, the fate of the fish significantly influenced the SGR in the linear mixed effects model. Fish that survived for the duration of the

experiment had a significantly higher SGR1 than those that died between week two and week four ($\chi^2 = 31.46$, $p < 0.0001$, model $R^2 = 0.26$). SGR1 was 0.69 ± 1.45 %/day for the fish that survived ($n = 72$), and -1.19 ± 0.82 %/day for fish that died ($n = 24$; Figure 3.1). Density, ration and their interaction did not significantly influence the SGR1 in the model. Among survivors, density, ration and their interaction did not significantly predict the SGRs in the linear mixed effects model (model $R^2 = 0.02$). Surviving fish grew at a rate of 1.94 ± 0.97 %/day over four weeks.

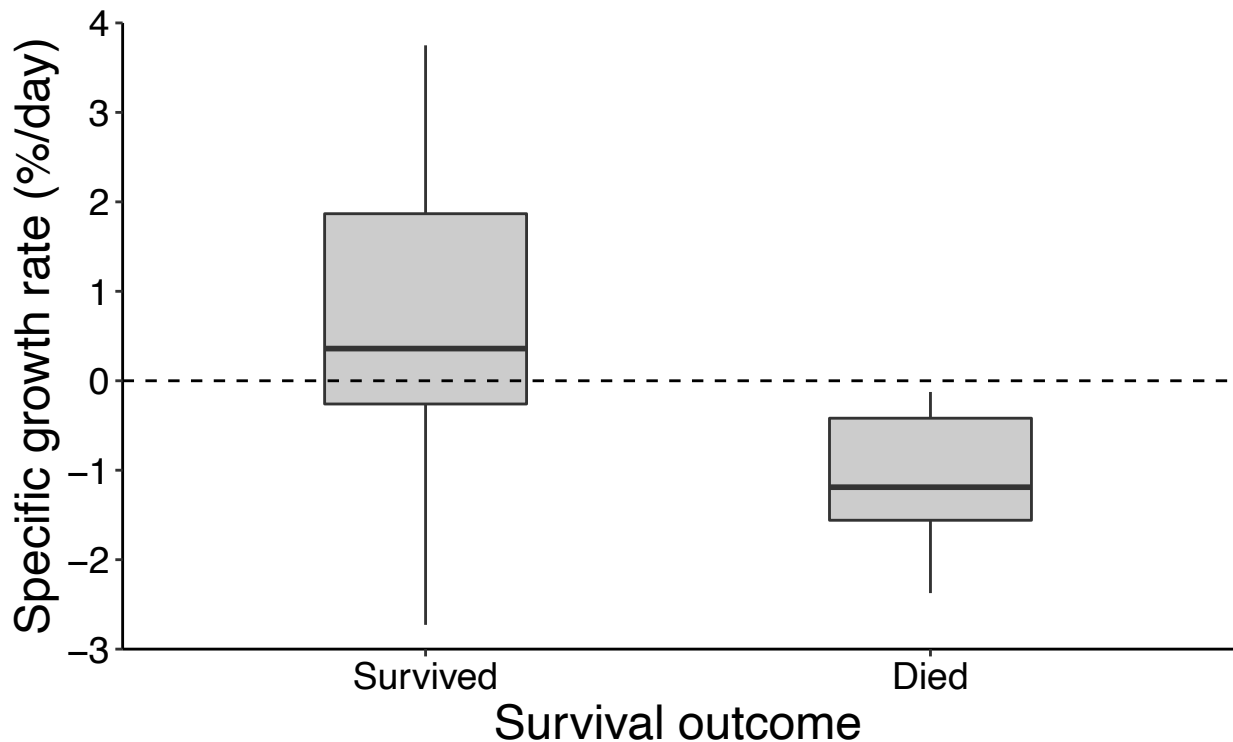


Figure 3.1 The specific growth rate of juvenile white sturgeon during the first week of the experiment. The survival outcome, whether the fish survived for the duration of the experiment or died in the subsequent weeks of the study, significantly influenced the growth rate. Fish that survived for the duration of the four-week experiment ($n=72$) grew significantly more than fish that died in weeks two to four ($n=24$). The boxplot represents the median and 25th and 75 percentiles. Whiskers are the smallest and largest values within $1.5 \times \text{IQR}$ of the percentile value. The dashed line indicates a growth rate of zero.

The tank growth efficiency was significantly higher for treatments that were fed at a half ration and explained 45% of the variance in the linear model ($F = 7.15$, $p = 0.015$, model $R^2 = 0.67$; Figure 3.2). Growth efficiency in half ration tanks was nearly twice as efficient as full ration tanks, 1.61 ± 0.21 and 0.96 ± 0.31 , respectively. Density and the interaction between density and ration did not have a significant effect on the growth efficiency.

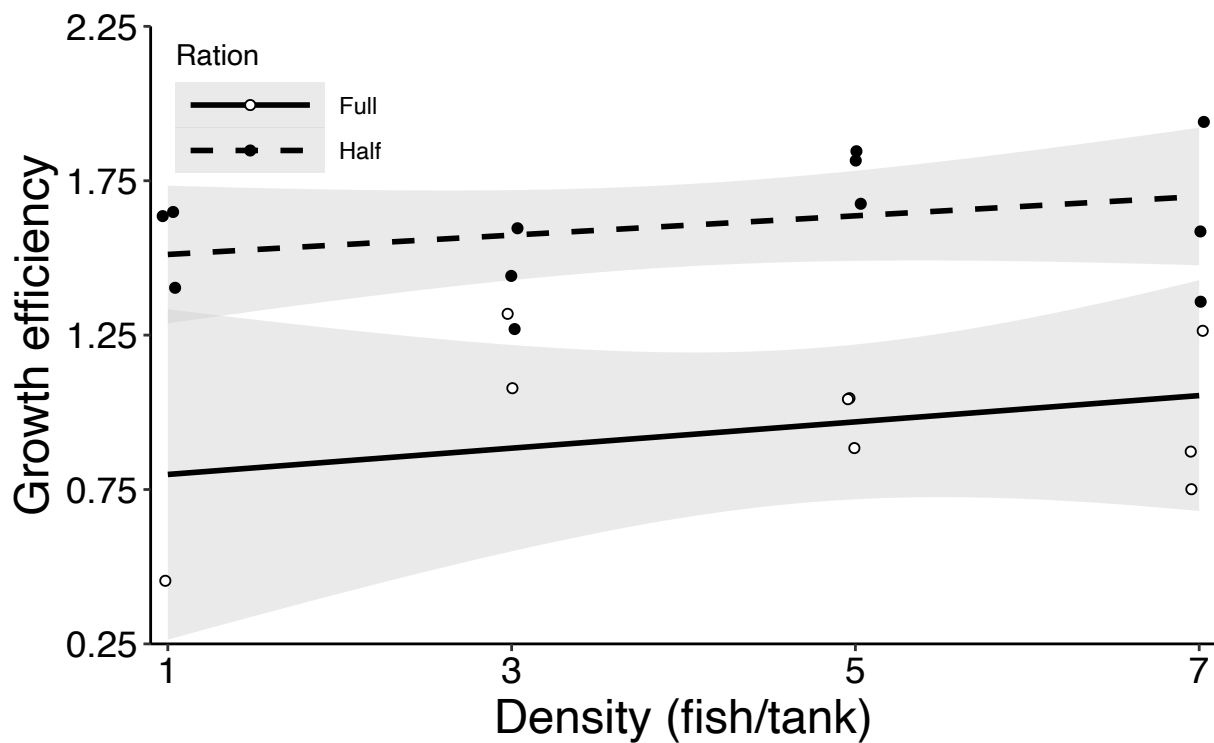


Figure 3.2 Per-tank growth efficiency of juvenile white sturgeon over the four-week experiment duration. Fish in treatments that were fed at half ration grew significantly more efficiently than tanks fed full rations. Density did not have a significant effect. Bands indicate the 95% confidence interval.

Density significantly influenced the mortality rates and explained 20% of the variance in the linear model ($F = 13.99$, $p = 0.001$, model $R^2 = 0.48$; Figure 3.3). Ration and the

interaction between density and ration did not have a significant effect on the mortality rate. However, the interaction between density and ration explained 25% of the variance in the model. In tanks with a single fish, the mean mortality rate was 0%. In the high-density treatments with 7 fish/tank, the mean mortality rate was $30.9 \pm 14.0\%$.

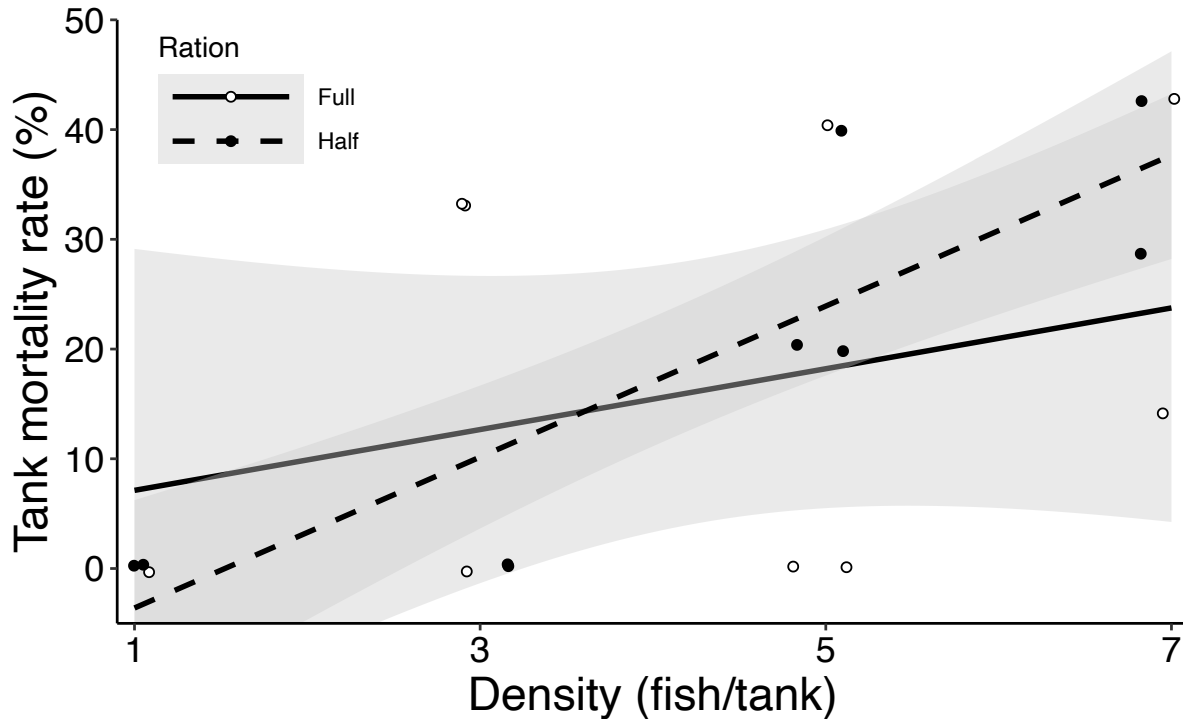


Figure 3.3 Mortality rate per tank of juvenile white sturgeon over the four-week experiment duration. Mortality rate significantly increased with tank density. Bands indicate the 95% confidence interval.

The final masses for both the survivors and mortalities were best predicted by the initial masses in the linear mixed effects models. The final masses of the mortalities ranged from 1.949 to 3.598 g with a mean of 2.738 ± 0.413 g (Figure 3.4A). Final mass was positively related to initial mass ($\chi^2 = 13.616$, $p < 0.0001$). Initial mass of the mortalities accounted for 85% the variation explained in the model, with a model R^2 of 0.41. The

final masses of survivors ranged from 2.470 to 10.897 g with a mean of 6.001 ± 1.987 g (Figure 3.4B). Final mass was positively related to initial mass ($\chi^2 = 54.462$, $p < 0.0001$). Initial mass accounted for 95% the variation explained in the model, with a model R^2 of 0.459. Density, ration and their interaction did not significantly influence the final mass of the survivors. Density, ration and their interaction, and the number of days the fish survived did not significantly influence the final mass of the mortalities.

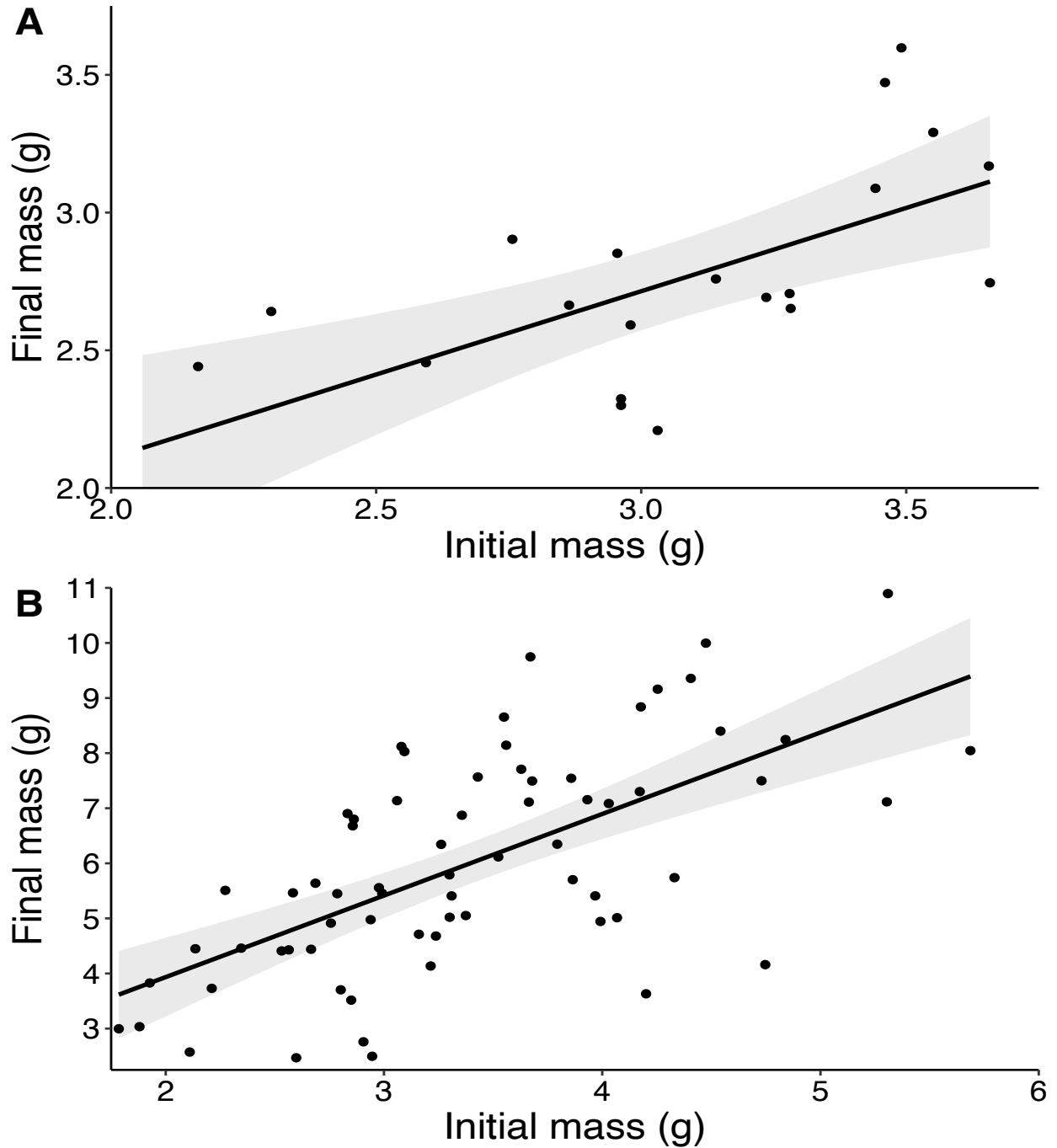


Figure 3.4 Final mass of the juvenile white sturgeon that A) did not survive to the end of the four-week study period and B) survived to the end of the four-week study period. Final mass was best predicted by the initial mass in both linear models. Bands indicate the 95% confidence interval.

3.4 Discussion

In my tests of juvenile white sturgeon growth rates, the best predictor of growth during the first week was survival outcome, and the treatment factors of density and ration did not significantly influence the SGR_1 . Fish that died during the study lost mass at an average rate of approximately -1 %/day during the first week of the study, whereas fish that survived gained approximately 0.7 %/day. Of the white sturgeon growth rate studies I reviewed, I did not find any incidences of measurement of growth outcomes for fish that did not survive. I found that surviving fish grew approximately 2 %/day over the four-week duration of my study, regardless of density or ration treatment. In their study of temperature and ration effects on feeding larval and early juvenile white sturgeon growth rates, Rodgers et al. (2018) found growth rates of approximately 3 %/day at 100% of the OFR and 1 %/day at 40% of the OFR at 11 °C. At 18 °C, fish grew at 6 %/day and 4 %/day at 100% OFR and 40% OFR, respectively. Though I used a similar experimental design to Rodgers et al. (2018), there were some key differences. The OFR model used by Rodgers et al. (2018) yielded higher feeding rates than the Cui and Hung (1995) model I selected for this study, resulting in approximately 35% more feed for their optimal ration. Additionally, and perhaps more critically, Rodgers et al. (2018) used younger fish in their study, beginning their trial at 32 dph (0.25 g average mass). Though this is only a month and a half younger than the fish used in my trials, the growth rate of juvenile white sturgeon quickly declines as body size increases. Deng et al. (2003) tested similar aged fish used in Rodgers et al. (2018) and estimated that 28-35 dph larvae (0.25 g average mass) grew at a rate of 10 %/day when fed at their OFR at 18 °C. De Riu et al. (2012) tested juveniles of a similar size as my initial body masses

(2.8-4.5 g) and found juvenile white sturgeon had growth rates of approximately 7 %/day when fed for a week at their OFR. This represents a difference in initial SGR of approximately 30% between the size of the larvae used in Rodgers et al. (2018) and those used in my in my study. Finally, Rodgers et al. (2018) allowed for an acclimation period of 5 days in the experimental units before starting the trial, whereas I began the trial immediately after transferring fish to the experimental units. The growth rate of survivors in my study was low in the first week (0.69 %/day), but quickly increased to approximately 2 %/day for the remaining weeks of the trial. Had I allowed for acclimation in the experimental units after the stress of the transfer, the growth rate during the first week of my experiment would have likely been higher.

I chose a water temperature of 13.5 °C as it is approximately the temperature that juvenile white sturgeon in the Nechako River would experience in September and October, coinciding with the study period (Fisheries and Oceans Canada 2014; Environment Canada 2020). This is significantly lower than temperatures used in aquaculture of white sturgeon. I found studies of growth in juvenile white sturgeon were often conducted at temperatures between 18 °C and 26 °C, with a suggested optimal temperature for growth at 23 °C (Hung et al. 1993; De Riu et al. 2012; Lee et al. 2016). These temperatures expedite growth and maturation but are higher than what juvenile white sturgeon would regularly experience in much of their range (Coutant 2004). Consequently, the results from these studies likely yield growth rates far beyond what could be observed in the wild.

Cui et al. (1997) found that growth rates were not only dependent on ration level, but also the timing of feeding. For the same ration level, fish that were fed more frequently grew faster. When the ration was fed over 24 hours, three-month-old white sturgeon grew at a rate of 3.6 %/day at 18.5 °C. Conversely, when fed their ration in two or four meals per day, the fish grew 2 %/day and 3.5 %/day, respectively. In contrast to Cui et al. (1997), I fed the ration in three meals per day and observed a mean growth rate of 2 %/day at a lower temperature of 13.5 °C. Had I increased the number of meals per day, I may have observed higher growth rates for the same ration. It has been suggested that sturgeon are continuous foragers in the wild, and therefore may benefit from continuous feeding regimes (Findeis 1997). This feeding strategy is used by other benthic-associated opportunistic omnivorous fish, including some *Cottus* and *Catostomus* species (Pearson and Healey 2003; Chalupnicki and Johnson 2016). Because of the small number of fish in my treatments, it was not feasible to divide rations into smaller meals. Additionally, fish were fed manually rather than using automatic feeders that are common in aquaculture and were fed exclusively during the day to simplify husbandry. Juvenile white sturgeon have higher activity levels at night in situ and in laboratory studies, though this is often attributed to predator avoidance rather than a feeding strategy to encounter nocturnal prey (Kynard and Parker 2005; Parsley et al. 2008; Steel et al. 2019). However, it is unlikely that a different feeding schedule would have affected my results as Cui et al. (1997) found that their juvenile white sturgeon grew at an equal rate whether fed exclusively during daylight or nighttime hours.

Growth was found to be twice as efficient in the treatments that received 50% of the optimal feeding rate in my study. As allocation of food resources between individuals within a tank was not tracked, growth efficiency was calculated on a per-tank basis. Though this method is not as accurate as measuring bioenergetics on an individual level, the growth rate results of this study support the inference that average efficiency was higher in the half ration treatments. Growth rates across the entire study period were not significantly different among survivors in both full and half ration treatments (approximately 2 %/day). My results of higher efficiency at reduced rations are consistent with findings of aquaculture studies of juvenile sturgeon. In their study of 360 g young-of-the-year white sturgeon, Lee et al. (2016) found that efficiency was highest in fish fed at half of their calculated optimal feeding rate (growth efficiency of 1.18 at a feeding rate of 0.8 %/day). At their optimal feeding rate of 1.5 %BW/day, growth efficiency was nearly half as efficient at 0.688. Similar results were found by Hung et al. (1993) in investigations of the influence of feeding rate and temperature on the growth and condition of 30 g white sturgeon. At both 23 °C and 26 °C, the growth efficiency was highest at the lowest feeding rates. Conversely, De Riu et al. (2012) found that growth was least efficient at the lowest feeding rates tested in white sturgeon aged 60 to 81 dph. As feeding rate increased to intermediate levels (at approximately 75% of the OFR), efficiency increased to a maximum and subsequently declined as feeding rate continued to increase up to and beyond their calculated OFR.

Low efficiencies at maximum feeding rates were consistent across many studies, indicating that maximizing growth rates may come at a higher food cost in aquaculture,

but may be best to improve nutritional status (Lee et al. 2016). Ration levels in my study were chosen at the most conservative level to avoid overfeeding the restricted-ration treatments and assuming that all fish in the full ration treatments would eat at their optimal rate to maximize growth. However, juvenile white sturgeon are able to eat at rates beyond their optima, resulting in diminishing returns on growth (De Riu et al. 2012). Sturgeon will eat to physical satiation if food is available, but the higher feeding rate will not result in higher growth due to declining growth efficiency (Lee et al. 2014). Growth efficiency in fish is primarily controlled by body size and ration (as reviewed in Paloheimo and Dickie 1966). In studies where individuals are of similar size, growth efficiency is negatively related with ration level and ration level is the best predictor of efficiency. In studies with inter-individual variability in body size, ration level is also correlated with efficiency, but size was the best predictor of efficiency. However, when Paloheimo and Dickie (1966) applied corrections to control for the variability in body size, ration again became the best predictor of growth efficiency. Thus, further investigations to track individual consumption rates and consideration of body size are needed to parse out the contributions of drivers of growth efficiency in juvenile white sturgeon.

My experiment yielded increasing mortality with increasing fish density. In tanks with one fish, mortality rate was zero, increasing to 30% in tanks with 7 fish, regardless of ration. In my review of the literature, I found that juvenile sturgeon mortality rates in aquaculture studies were often low or unreported, and up to 10% mortality was considered acceptable (Cui et al. 1997; Köksal et al. 2000; De Riu et al. 2012). In the

few examples of analysis of mortality rates, the evidence for density influencing juvenile sturgeon mortality rates was mixed. In their investigation of the effect of rearing density on growth and mortality rates in juvenile (368 g) Atlantic sturgeon (*A. oxyrinchus oxyrinchus*), Jodun et al. (2002) found that mortality rates were negligible and not associated with tank density. In contrast, Mohler et al. (2000) found increasing mortality rates with fish density for fingerling Atlantic sturgeon, nearly doubling from 6.7% in tanks with 0.5 fish/L to 13% at densities of 3.2 fish/L. Mortality rates between studies of Amur sturgeon (*A. schrenckii*) also varied. Ni et al. (2016) found that stocking density of 40 g sturgeon did not influence mortality rates, whereas Zhu et al. (2011) found increasing mortality as densities of 50 g fish increased even at densities lower than those tested in Ni et al. (2016). As mortality increased with density at the same rate regardless of ration in my study, it is possible that good competitors ate beyond their OFR to physical satiation in the 100% OFR treatments leading to the exclusion of weaker competitors and inefficient growth. Even so, the evidence in the aquaculture literature of density dependent mortality is highly conflicted and mechanisms remain unclear. Investigations into the behaviour of sturgeon in these environments at various densities may elucidate the mechanisms to explain such variance in outcomes between studies.

Intraspecific competition in the early life history stages of sturgeon is of great interest to conservation biologists seeking to better understand population dynamics and inform hatchery stocking strategies. However, direct investigations of behavioural interactions and their consequences for growth rates has rarely been quantified in the literature. In their study of foraging in juvenile Atlantic and shortnose (*A. brevirostrum*) sturgeon,

Kynard and Horgan (2002) observed larger fish charging, biting or pushing smaller fish out of tank regions with high foraging opportunity early in their study. Once the dominance hierarchy for tank regions was established, the aggressive behaviours diminished over the study period and large fish consistently occupied optimal foraging regions. This pattern was not observed in my study. Though I did not quantify interactions between fish during the study, behavioural observations during feeding did not yield evidence of overt aggressive behaviours or establishment of territories by large, dominant fish. Similar findings have been observed in juvenile lake sturgeon (*A. fulvescens*), with some evidence that presence of conspecifics can be beneficial for attenuating stress (Allen et al. 2009; Hare et al. 2015). During feedings, food was evenly distributed across the tank, minimizing the establishment of regions with consistently high foraging opportunity. Spatial distribution of food resources has been found to change the nature of competitive interactions in other fish species. Shifts from interference competition when resources are spatially concentrated to scramble competition when resources are dispersed have been observed in medaka (*Oryzias latipes*; Magnuson 1962; Bryant and Grant 1995), chum salmon (*Oncorhynchus keta*; Ryer and Olla 1995), convict cichlids (*Cichlasoma nigrofasciatum*; Grant and Guha 1993) and Everglades pygmy sunfish (*Elassoma evergladei*; Rubenstein 1981). Sturgeon swimming speed (Cheong et al. 2006) and gape (Carroll and Wainwright 2003) also increase with body size, potentially allowing larger fish to reach and consume food faster than their smaller competitors in scramble competition (Ward et al. 2006).

In their investigation of feeding relationships in juvenile stellate (*A. stellatus*) and Russian (*A. gueldenstaedtii*) sturgeon, Sbikin and Budayev (1991) found that larger individuals of both species spent more time on the bottom of the tank. They noted that the sturgeon randomly collided due to high levels of swimming activity, thereby displacing smaller fish into the water column. Though these collisions were considered random rather than deliberate acts of aggression, they resulted in a hierarchy where large fish monopolized food resources on the bottom of the tank and expended less energy swimming, leading to disproportionately higher growth. I found that SGR in the first week of the study was best predicted by the survival outcome of the fish, rather than fish density or ration. Fish that survived to the end of the study gained mass during the first week of growth, whereas fish that died lost mass. This indicates that some fish may have had their feeding opportunities limited early in the study, resulting in mass loss and eventual death. I observed a pattern of fish spatial distribution similar to the results described by Sbikin and Budayev (1991). In the high-density tanks with seven fish, four or five of the fish appeared to remain close to the bottom of the tank and the remaining fish swam in the water column. If the same fish occupied the bottom of the tank for the duration of the experiment, they may have consistently excluded their tankmates from foraging opportunities. This observation, in conjunction with the association of mortality rates to fish density regardless of ration, could suggest that few fish monopolize food resources and decrease the growth and survival of their competitors.

Although the effect of density, feed ration and feed timing have been intensively studied for white sturgeon under aquaculture conditions to maximize growth and profitability (See Hung et al. 1993; Cui et al. 1997; De Riu et al. 2012; Lee et al. 2014 as examples), little effort has been invested in extending these findings to wild sturgeon populations. The relevance of competitive behaviours in artificial environments to behaviours in the wild has been debated. Sbikin and Budayev (1991) argue that their findings of a size hierarchy forming in treatments with low benthic area were a result of artificial densities that would not be relevant in the wild. Kynard and Horgan (2002) assert that while artificial densities in aquaculture may intensify agonistic interactions, species that exhibit dominance hierarchies in artificial conditions also exhibit those behaviours in the wild. Behavioural observations and manipulative experiments in situ are needed to support the assertion that resource availability affects sturgeon in the wild (Kynard and Horgan 2002; Barth and Anderson 2015).

Though intraspecific competition in juvenile sturgeon has not been studied directly as a driver of population dynamics in the wild, it has been hypothesized as a factor contributing to observed trends of age- or size-specific mortality rates. In the Kootenai River, size- and density-dependent factors have been suggested as contributors to increasing mortality rates of hatchery released, juvenile white sturgeon (Justice et al. 2009). In the first seven years of hatchery releases, one-year post-release survival was an average of 72% irrespective of body size. As hatchery strategy shifted to releasing greater numbers of smaller juveniles in 2002, survival of juveniles declined to a mean of 27% in the following years. The decline in survival has been attributed to competition

within the release cohort for food resources and potential cannibalism from older age classes from prior releases. These trends were not found in older, larger (>25 cm) juveniles, suggesting that releasing fewer, larger juveniles may reduce competition for food and predation, leading to better outcomes in the wild. Steffensen et al. (2019) have found similar results for pallid sturgeon (*Scaphirhynchus albus*) in the Missouri River. Survival in juveniles released at age-1 has declined 2.5 times in recent years, whereas survival in juveniles released at age-2 or greater has not changed. The Missouri River also has a large population of shovelnose sturgeon (*S. platyrhynchus*), potentially intensifying competition through interspecific interactions.

In conclusion, growth and survival outcomes of age-0 white sturgeon in this laboratory study were most influenced by initial body condition and the corresponding competitive advantage to exploit food resources, rather than ration. These results differ from the aquaculture literature, as groups of individuals in aquaculture are homogenized by size and weak individuals are removed. Fish that died during the trial had smaller initial masses than survivors and lost mass before they died. The association of increasing mortality rates with increasing density, and the comparative growth performance of surviving fish in both limited and full ration treatments, suggests that good competitors are able to exploit food resources and reduce the growth and survival of weaker competitors. Dominance hierarchies are common in carnivorous fishes and are often established with aggression (Ward et al. 2006). However, a dominance hierarchy was not observed in my study. Contest competition leading to a dominance hierarchy has been posited as a contributing factor to patterns of growth variability in both aquaculture

and in the wild for juvenile white sturgeon, yet evidence to support this relationship is inconclusive. Further investigations into food resource availability and intraspecific competitive interactions in the wild are needed to establish causative relationships to observed demographic trends and extend laboratory findings to populations in situ.

Chapter 4: Discussion

In this thesis, I explored how food availability and intraspecific competition for food influenced the growth and survival of the larval and early juvenile stages of white sturgeon. The goal of this thesis was to address two knowledge gaps identified in the Canadian species recovery plan, i.e., basic biological information on the early life history stages and factors contributing to ongoing recruitment failure (Fisheries and Oceans Canada 2014). Spawning is occurring annually, and the eggs collected from spawning events appear to be largely viable (Howell and McLellan 2007; Triton Environmental Consultants 2009; Paragamian 2012). Additionally, post-release survival of age-1 hatchery juveniles is generally high (Ireland et al. 2002; Irvine et al. 2007; Justice et al. 2009). Therefore, recruitment failure is likely occurring during the larval and early juvenile stages. Recently, mechanisms to explain the decline in survival rates of these stages, including geomorphic change, insufficient food supply, and loss of habitat diversity, have been proposed (McAdam 2015; Hildebrand et al. 2016). Efforts to directly test these mechanisms have been mostly limited to laboratory studies, as detecting these stages in the wild is rare and in-situ experiments on these small and sensitive organisms are logistically challenging (COSEWIC 2012). Although the findings of my laboratory studies are not representative of the complexity of conditions sturgeon experience in the wild, they allowed me to directly observe the early life history stages and collect evidence that could support or refute some of the proposed mechanisms of recruitment failure.

In Chapter 2, I investigated how the presence of substrate and the timing of food availability during the transition from endogenous yolk sac (YSL) stage to exogenous feeding (FL) stage affected growth and health outcomes of larvae. I found that the presence of substrate during the YSL stage was beneficial for the growth of larval white sturgeon in both the YSL and FL stages. I also found that FL were highly resilient to starvation. Larvae survived up to the last starvation treatment used in my experiment, 18 days of starvation, and were able to gain weight after the initiation of feeding. Against expectations, the survival rates of larvae were similar across all treatments. The PNR metric for assessing the starvation resistance may therefore not be appropriate for white sturgeon larvae. The PNR hypothesis was developed for marine larvae that have limited yolk supply and short critical periods before mortality rates sharply increase (Hjort 1926; Blaxter and Hempel 1963). As reviewed in Chapter 2, starving sturgeon larvae do not exhibit this pattern. Instead, sturgeon larvae exhibit slow increases in mortality rates as starvation periods are extended, with the majority of starving larvae dying before the classical definition of the PNR is reached. Therefore, more evidence is needed to understand the magnitude of starvation resistance for white sturgeon and support the starvation hypothesis as a significant contributor to recruitment failure.

In Chapter 3, I investigated the role that intraspecific competition plays in influencing growth and mortality rates in age-0 (3-month-old) juvenile white sturgeon. I observed comparable growth rates among surviving fish across all density and ration treatments. Final mass at the end of the study was best predicted by initial mass, suggesting that initial condition is important for competitive ability. Additionally, mortality rates increased

with fish density and was independent of ration. I infer that these results are the consequence of good competitors fully exploiting food resources. This exploitation likely resulted in the exclusion of weaker competitors from feeding opportunities in tanks with high densities, leading to poor growth outcomes and elevated mortality rates.

Intraspecific competition between juvenile sturgeon in the wild is a concern for management and has been proposed as a limiting factor for recovering populations. However, in spite of such concerns research in this area is limited, and more research into the nature of competitive interactions of juvenile sturgeon and their potential to explain observed growth patterns of wild juveniles is needed.

I found that resource limitation affects multiple stages in the early life history of white sturgeon. In the YSL stage, the absence of suitable hiding habitat leads to increased energy expenditure for locomotion and diminishes allocation to growth and development. After transition to exogenous feeding during the FL stage, larvae with immediate access to high quality food sources had higher growth. Although FL are highly resistant to starvation, even short periods of food limitation gave the larvae a growth disadvantage that they did not recover from during the FL stage. Young white sturgeon also suffer from carryover effects from facing hardships in previous life history stages. I found that FL reared without substrate during the YSL stage had lower growth rates than FL reared with substrate, despite having equal feeding opportunities.

Additionally, I found that smaller juvenile sturgeon were poorer competitors for food resources and resulted in limited growth. If food limitation during the FL stage leads to smaller juvenile size after metamorphosis, these fish may be at a competitive

disadvantage for feeding opportunities. Diagnosing resource limitations in the wild may therefore be challenging for white sturgeon, as carryover effects can obscure when the young-of-the-year fish experienced the limiting stage and white sturgeon may face multiple of these bottlenecks throughout the first year of their life. Ultimately, these limitations may cumulatively impact recruitment rates.

4.1 Implications and Future Directions

Sturgeon are among the most endangered fish in the world, with 63% of the 26 species classified as critically endangered (Pikitch et al. 2005; Haxton et al. 2016). To compensate for the decline of natural stocks, sturgeon aquaculture to produce caviar and meat, and to enhance wild populations, has increased rapidly over the last three decades (Bronzi et al. 2011; Chebanov et al. 2011). My results can inform aquaculture practices for larval and juvenile white sturgeon rearing. First, my results indicate that growth and survival of larval white sturgeon are not greatly affected by a few days of starvation between the complete exhaustion of the yolk sac and the initiation of exogenous feeding. The transition to exogenous feeding is a critical time during the early life history of sturgeon. For artificial propagation, little information exists on the timing to initiate feeding for larvae to maximize growth and survival (Gisbert and Williot 1997). Uncertainties around the ability to feed before the exhaustion of the yolk sac, the behavioural or morphological cue to signal readiness to feed, and the consequences of not feeding precisely when larvae are ready, have led to inconsistent recommendations for the timing of first feeding (Conte et al. 1988; Dettlaff et al. 1993; Gisbert and Williot 1997). As a precautionary measure to address these uncertainties, larvae are often first

fed several days before the complete exhaustion of the yolk, but the efficacy of this measure has been debated (Gisbert and Williot 2002; Chebanov et al. 2011). My work suggests that feeding before the exhaustion of the yolk sac would not lead to a significant benefit in survival and a marginal benefit in growth rate. As I fed my larvae at the first observation of melanin plug ejection, it is likely that many larvae still had some remaining yolk when I began feeding the 11 dph treatment group. The larvae fed at 11 dph and at 14 dph had comparable mortality rates and the 11 dph group only grew slightly faster. Based on my results, I would not recommend feeding larvae before the exhaustion of the yolk sac. Feeding larvae early would generate unnecessary food costs and could increase the risk of disease (Chebanov and Galich 2011; Chebanov et al. 2011). Future work should directly investigate the timing and ontogeny of the initiation of the FL stage for white sturgeon and the potential benefits or detriments of early feeding for aquaculture practices. Additional work is also needed to understand the sublethal effects of food limitation and starvation on surviving larvae, and if these effects impact the success of sturgeon long term as they develop into juveniles.

Second, I found the presence of substrate during the YSL stage to be beneficial for the growth of white sturgeon larvae. Larvae reared in substrate were heavier at the initiation of feeding and grew faster over the total duration of the experiment. Despite expanding evidence that substrate can be beneficial for the growth, development and survival of sturgeon species that use complex substrates during the larval stages in the wild, the use of substrate is uncommon in sturgeon aquaculture (for example, Gessner et al. 2009; Baker et al. 2014; Bates et al. 2014; Boucher et al. 2014). Natural rock substrates

are heavy and represent a bio-security risk, as they cannot be cleaned effectively during larval rearing without crushing the larvae hiding in the interstitial spaces. The presence of an artificial substrate that is lightweight, more structurally complex per volume than rock and is easy to clean, could provide growth and development benefits to larvae while costing very little. I recommend adopting the use of substrate for the artificial propagation of sturgeon that require interstitial habitat for their larval stages.

Finally, I found that juvenile white sturgeon competing for food have poorer growth and survival outcomes than those reported in the white sturgeon aquaculture literature. A lack of basic biological information on the ecology of the early life history stages of white sturgeon hinders the ability to target conservation efforts to the stages that are most vulnerable (COSEWIC 2012). Without ecological information, managers may rely on growth and mortality data from the aquaculture literature. My results, though limited in their extensibility to wild conditions, indicate that growth rates in aquaculture are likely much higher and mortality rates are much lower than that those experienced by juveniles in the wild. Aquaculture operations employ strategies to minimize competition for food and maximize growth rates, including size homogenization and removal of weak competitors (Chebanov et al. 2011). In my study, I used a wide range of sizes where my largest fish was over three times larger than the smallest fish and fish were only removed upon death. To better understand the growth potential and mortality rates of wild juvenile white sturgeon, intensive population monitoring is needed. Additionally, more behavioural research into the dynamics of feeding juvenile white sturgeon is needed to describe their intraspecific competitive interactions. I did not observe any

obvious signs of aggression between fish to defend food resources, but more subtle interactions may explain my observed growth and mortality patterns (for example, displacement of smaller fish into the water column; Sbikin and Budayev 1991).

My results suggest that habitat restoration actions could help both larval and juvenile stages of white sturgeon life history. In the absence of a definitive causal mechanism for recruitment failure, habitat restoration efforts could address several of the proposed recruitment failure hypotheses. Population growth may also be limited by more than one life history stage. Increasing habitat quality and quantity for not only the most limited stages but also their subsequent stages can have a positive effect on overall fish population size, so targeting conservation efforts to all of the early life history stages may be beneficial (Rosenfeld and Hatfield 2006). First, substrate restoration in spawning grounds may increase survival in the egg and larval stages (McAdam 2012; Crossman and Hildebrand 2014). The addition of coarse sediments or the removal of fine sediments from the existing spawning beds could reduce the mortality risk of egg smothering by fine sediments and provide interstitial hiding spaces for YSL (Kock et al. 2006). The artificial substrate used in my study approximated the interstitial spaces of coarse sediment spawning beds historically used by YSL in the wild. The YSL reared without interstitial hiding spaces, approximating highly embedded coarse substrate or fine substrate-dominated spawning beds found in dam-modified rivers, performed comparatively worse in both the YSL and FL stages. The YSL with access to interstitial habitat also have lower predation risk, higher growth rates and initiate downstream drift

later and less synchronously, all of which could increase survival (McAdam 2011; Crossman and Hildebrand 2014; Boucher et al. 2014).

Restoring side channel habitat may also benefit the early life history stages of white sturgeon. There is evidence of adults spawning outside of the main channel of the river in some populations, with eggs and larvae found in side channel habitat (Perrin et al. 2003). Side channels are also critical habitat for early juvenile white sturgeon (Bennett et al. 2005). The modification of large river systems from increasing industrialization, including damming, diking, and bank armoring, has led to the fragmentation and drastic loss of side channel habitats that act as nurseries for juvenile sturgeon (Parsley and Beckman 1994). Because of this habitat loss, juvenile sturgeon may face increased intraspecific competition for limited space or food resources. My results suggest that when faced with limited resources, dominant fish monopolize resources and exclude weaker competitors. Restoring side channel habitat could have the potential to increase juvenile white sturgeon growth and survival in the first year of life. Conservation aquaculture has been a valuable tool to enhance juveniles in populations suffering from recruitment failure, but the ultimate goal for the recovery of white sturgeon in Canada is self-sustaining, naturally reproducing populations. As the focus of conservation efforts transitions from conservation aquaculture to habitat restoration, understanding the biology and habitat requirements of white sturgeon during their first year of life is essential to restore population recruitment.

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