**Growth Rate and Size Variability among Juvenile
Lake Sturgeon, *Acipenser fulvescens*: Implications for Recruitment**

by

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Abstract

      There is a growing recognition that conservation programs using hatchery-reared fish should strive to produce individuals that represent phenotypes present in natural environments. Size variability within cohorts, mediated through inter-individual differences in growth rates, provides one avenue by which phenotype can be studied. High growth rates are generally equated with greater fitness. However, there is evidence that fish with slower relative growth and smaller sizes continue to persist within populations. This thesis aimed to better understand the causes and potential implications of variable sizes and growth rates on the potential recruitment of hatchery-reared Lake Sturgeon, *Acipenser fulvescens*. Studies were developed to 1) determine the mechanisms behind these observed variations and 2) assess the behavioural and physiological consequences of being either a fast- or slow-grower (i.e., large or small). Laboratory studies concluded that external factors, most notably the presence of conspecifics during feeding events, influenced size variability more than inherent predispositions towards faster or slower growth. Examination of size-dependent versus size-independent feeding interactions further confirmed that variability does not appear to be the result of underlying fixed behaviours. The consequence of slower growth rates and smaller sizes did not lead to higher mortality or reduced body condition during a low temperature challenge. Recapture rates and downstream movements following stocking events of both young-of-the-year (YOY) and yearling Lake Sturgeon in the Winnipeg River, Manitoba could not be correlated to inter-individual differences in size. Although initial study on the cause of growth and size divergence may lead one to conclude that slow-growing

(i.e., small) Lake Sturgeon represent a substandard phenotype, subsequent studies could not point to inferior performance of these individuals when compared to faster-growing (i.e., large) individuals of the same age. As such, the practice of size-selection for relatively faster-growing and larger individuals in future Lake Sturgeon enhancement programs is discouraged, at least until there are more conclusive findings to suggest otherwise. Future studies should continue to look at recruitment in relation to growth rate and size among naturally produced Lake Sturgeon juveniles in order to put the results of this research into context.

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CHAPTER 1

General Introduction

Background

Growth and size variability in fish

Following hatch, growth among larval fish is critical in order to decrease their

susceptibility to potential predation and to increase the variety of prey available for

consumption (Osse et al. 1997). It should come as no surprise then that growth rates are

at lifetime highs during early development. For example, the dry body mass of some

teleost fish such as Turbot, *Scophthalmus maximus*, and mackerel, *Scomber* sp. can

increase 100-fold in only three weeks following hatch (Nellen 1986). High growth rates

are also particularly important in north-temperate environments where overwinter

survival depends on adequate body reserves (Cargnelli and Gross 1997; Biro et al.

2004a). Indeed, organisms with high growth rates are generally assumed to have greater

fitness, and life-history theory has generally assumed that juvenile growth rates are near

their physiological maximum (Stearns 1992; Sogard 1997). Yet, there is increasing

evidence to suggest that slower growing organisms may not necessarily be at a fitness

disadvantage. For instance, despite what would appear to be similar and optimal growing

conditions, individuals within a cohort often display variable growth rates (Martins et al.

2005).

Persistent individual growth variation has been documented (Pfister and Stevens

2002), and explained through tradeoffs of the benefits of increased growth rates with

compromised antipredator behaviour, somatic development, immune function, and

responses to physiological stressors (Arendt 1997; Mangle and Stamps 2001). Studies

assessing growth rate variability are generally completed in two phases. Initially it is the

mechanism producing variability that is of interest, followed by the study of its

persistence (or lack thereof) over time. Together, patterns of variability emerging from

such studies can provide valuable insight into the driving forces behind natural selection and fitness (Arendt and Wilson 2000).

Size variation within cohorts, resulting from inter-individual variability in growth rates, has been linked to a number of underlying physiological and behavioural differences that may become amplified by environmental conditions. Unequal competitive ability among individuals, in particular the formation of dominance hierarchies, is generally accepted as the major contributor to growth variability (Martins et al. 2005). Differences in activity, disproportional food acquisition and physiological stress among subordinates are three mechanistic hypotheses that have been used to explain the 'size hierarchy effect' (Brown 1946; Magnuson 1962; Allen 1972). Since first being proposed, a number of studies have been able to link growth variability to one or more of these mechanisms.

Koebele (1985) devised an elaborate experiment on a single family of juvenile cichlids, *Tilapia zillii*, to determine which of the three mechanistic approaches (i.e., activity, food acquisition and stress) could best explain growth variability. This was achieved by rearing fish under five different treatments: (1) individuals separated by transparent partitions only when fed, (2) individuals separated permanently by transparent partitions, (3) individuals separated permanently by opaque partitions, (4) individuals reared in groups and never separated, and (5) individuals reared in groups with unlimited rations. All study fish were provided dry pellets twice daily with total rations provided to study fish in treatments 1 to 4 being equal, while fish in treatment 5 received approximately 10 times more feed. Where study fish were held in compartments (i.e., treatments 1 to 3), the total ration was divided equally among fish. Results from this

study revealed that fish reared separately, either entirely (treatments 2 and 3) or during feeding (treatment 1), had the least amount of growth variability. In contrast, those treatments allowing social contact during feeding (treatments 4 and 5) led to the highest amount of growth variation. Of particular interest was the fact that individuals reared in treatment 5 (i.e., grouped with unlimited rations) displayed significantly more variable growth rates than all other treatments. This was explained by assuming the dominant individuals were still able to defend resources at the higher ration level. In fact, although not quantified, larger, dominant individuals within both treatments 4 and 5 were observed feeding first and consuming a proportionately higher amount of food than their tank mates. This led the author to conclude that the disproportional food acquisition hypothesis was the most likely mechanism creating a size hierarchy effect. More recently, studies conducted on juvenile Rainbow Trout, *Oncorhynchus mykiss* (Gregory and Wood 1998), and Turbot (Irwin et al. 2002), were able to show that growth variability was due to variation in feeding rates between dominant and subordinate individuals when reared in groups.

Jobling and Reinsnes (1986) conducted a study on the growth variability of stunted Arctic Char, *Salvelinus alpinus*. Fish were subjected to one of three treatments: (1) individuals reared in groups, (2) individuals separated by transparent walls and (3) individuals separated by opaque walls. In contrast to the earlier study by Keobele (1985), Arctic Char were found to exhibit greater growth variability when reared in isolation, regardless of divider type. The lower growth variability among grouped individuals was attributed to suppression of growth through social interactions. Abbott and Dill (1988) concluded that reduced growth among subordinate juvenile steelhead, *Oncorhynchus*

mykiss, reared alongside size-matched dominants, was due to 'psychological stress'.

Increased activity among dominant individuals is the third hypothesis proposed to explain the 'size hierarchy effect', but does not appear to explain size variability in and of itself. For instance, enhancing growth rates among Atlantic Salmon, *Salmo salar*, through genetic manipulation (Abrahams and Sutterlin 1999) or growth-hormone implants (Martin-Smith et al. 2004) did elevate competitive ability and elicit greater foraging activity. However, increased activity was also accompanied by increased food consumption in both these studies, which ultimately elevates growth rates among competitively superior individuals.

There is evidence to suggest that growth variability can emerge independent of competitive interactions. For example, Ojanguren et al. (1996) found a positive relationship between growth rates of juvenile Brown Trout, *Salmo trutta*, and initial body sizes at hatch. Likewise, Wang et al. (1998) found a positive relationship between initial body masses and specific growth rates (% d^{-1}) and gross growth efficiency, respectively, in juvenile hybrid sunfish (female Green Sunfish, *Lepomis cyanellus* x male Bluegill, *L. macrochirus*) reared in isolation. Faster growing young-of-the-year Atlantic Cod, *Gadus morhua*, were shown to be metabolically more efficient than fellow slow-growing individuals of the same cohort (Peck et al. 2004). An inherent basis for variation in feeding behaviour was demonstrated by Martins et al. (2005), when they showed that individual differences in feed intake/efficiency and total feeding time were repeatable within individuals over time.

Such studies have helped form and support the more recent idea of behavioural syndromes or 'personalities' (i.e., a suite of correlated behaviours reflecting among

individual consistency in behaviour across multiple situations; Sih et al. 2004). There is increasing evidence that inter-individual differences are adaptive. Dall et al. (2004) pointed out that different behavioural phenotypes within a species could affect how a population responds to change. For example, individuals within a population could be flexible in their response; however, costs to flexible behaviour (e.g., errors, response time-lags) favour a fixed proportion of individuals that are consistent in their behavioural phenotype. Reale et al. (2007) defined five major temperament trait categories: shyness-boldness, exploration-avoidance, activity, sociability and aggressiveness. These behaviours can greatly influence foraging behaviour and may explain why growth rate variability emerges (and persists) within cohorts, as was suggested by Stamps (2007).

As outlined, there are a number of ways that variable growth rates may occur within a cohort. Over time this variation can either remain the same, decrease (growth compensation) or increase (growth depensation; Pfister and Stevens 2002). Generally, fish of smaller sizes are considered to have fitness disadvantages, which would be expected to cause a gradual decrease in growth variability over time as smaller individuals dropped out of the population. Arendt (1997) listed a number of factors that select for high growth rates including: energetic demands of migration, short growing seasons prior to winter, competitive advantages and predation refuges. Yet, there are accounts of growth variability persisting within cohorts through time (Pfister and Stevens 2002). Tradeoffs between increasing growth and mortality have been used to explain these patterns within populations (Mangel and Stamps 2001). Previously reviewed in Arendt (1997), costs incurred from faster growth may include compromised somatic development (Arendt and Wilson 2000; Robinson and Wardrop 2002), swimming

capabilities (Farrell et al. 1997), immunity (Jhingan et al. 2003) and antipredator behaviour (Johnsson et al. 1996; Jonsson and Bjornsson 2002; Biro et al. 2004a, Biro et al. 2004b, Sundstrom et al. 2004; Biro et al. 2007).

Growth and size variability in sturgeon

Sturgeon are distinguished by their unusual life history of large adult sizes, late maturation, high fecundity and long life spans. Yet, despite the influence that growth rate can have on all of these features, surprisingly little research has specifically targeted sturgeon growth rate variability. Probing the literature does provide evidence of variable growth rates between and within sturgeon populations. For instance, growth rates for populations of Lake Sturgeon, *Acipenser fulvescens*, and Shortnose Sturgeon, *A. brevirostrum*, differ depending on their latitudinal location; the same has been observed in another acipenseriform, Paddlefish, *Polyodon spathula* (LeBreton and Beamish 2004). As observed in other species, sturgeon individuals within cohorts are known to display differences in growth rates under culture conditions (Monaco et al. 1981; Nathanailides et al. 2002; Qian et al. 2002). Variable growth rates also appear to persist in natural and stocked populations based on information from age-at-length plots for Gulf Sturgeon, *A. oxyrinchus desotoi* (Reynolds 1993 *in* Sulak and Randall 2002) and Lake Sturgeon (Barth 2011), seasonal length-frequency histograms constructed from Atlantic Sturgeon, *A. oxyrinchus oxyrinchus*, yearlings collected from the Hudson River (Peterson et al. 2000), length-frequency plots for young-of-the-year Shovelnose Sturgeon, *Scaphirhynchus platorynchus*, in the Missouri River (Braaten and Fuller 2007), data on recaptured juvenile White Sturgeon, *A. transmontanus*, following release in the Kootenai River (Ireland et al. 2002) and data on recaptured juvenile Lake Sturgeon released into Oneida

Lake (Jackson et al. 2002).

The mechanism(s) through which this size variability exists is not entirely clear. Gisbert et al. (2000) found that size variability among larval Siberian Sturgeon, *A. baeri*, was related to initial egg sizes (e.g., larger individuals hatched from larger eggs). However, growth rates were not found to vary in this study between the largest and smallest individuals and size was no longer correlated with initial egg diameter by the time fish from this study were juveniles. Qian et al. (2002) studied juvenile Chinese Sturgeon, *A. sinensis*, of differing sizes with respect to food intake and activity levels. Results indicated that growth rates were positively related to food intake, mediated by activity levels (i.e., distance moved and time spent swimming per day).

Social interactions are not well studied in sturgeon, despite their gregarious nature, but a few studies have indicated that physical interactions among juveniles may contribute to size variability. Sbikin and Budayev (1991) suggested that neutral intraspecific contact between juvenile Stellate Sturgeon, *A. stellatus,* under artificially created high densities contributed to size variability. They observed that larger juveniles were able to occupy valuable feeding space on the bottom of the tank while smaller individuals were 'pushed' into the water column away from food. The authors termed this behaviour "pseudo-hierarchic". Kynard and Horgan (2002) witnessed Shortnose Sturgeon and Atlantic Sturgeon displaying aggressive behaviour toward smaller individuals (e.g., charging, pushing, biting). However, these behaviours were not demonstrated in groups of Lake Sturgeon consisting of large and small conspecifics when quantified in a laboratory study (Allen et al. 2009).

Research by Nathanailides et al. (2002) provided an intriguing observation when

the progeny of a single cross (i.e., one male and one female) of Russian Sturgeon, *A. gueldenstaedtii*, produced high inter-individual variation in sizes following three weeks post hatch, regardless of hatching time (e.g., early-, mid-, late-hatch). This is a particularly relevant finding if a link between behavioural phenotype and growth rate can be made (Stamps 2007). Such a connection would further the idea that individual variation is the end product of natural selection and not just the raw material from which it acts (Wilson 1998). It might also help explain why species like sturgeon invest a considerable amount of time to growing large in order to release copious numbers of small eggs. For instance, female Lake Sturgeon are reported to produce approximately 11,000 eggs per kg of total body weight (Harkness and Dymond 1961), and the resulting offspring could potentially represent many different fixed behaviours. Termed "bet hedging" by Slatkin (1974), such a strategy is expected to occur when an individual may optimize fitness in highly variable spatial or temporal habitats. Some research has already provided evidence that different behavioural types of fish display superior performance under varying habitats. For example, dominant juvenile Brown Trout have higher fitness (i.e., growth rate) than subordinates when habitats are simple, whereas the results are reversed when fish are placed in complex habitats (Hojesjo et al. 2004). As most sturgeon species are under considerable threat (Peterson et al. 2007), many natural populations are supplemented with hatchery-reared fish (Chebanov et al. 2002; Ireland et al. 2002; Jackson et al. 2002). It is understood that maintaining high genetic diversity is important within these restoration attempts (Pikitch et al. 2005; Drauch and Rhodes 2007). If different behavioural phenotypes are present in sturgeon populations, and if such types outperform each other under particular situations, then maintaining phenotypic variability

within groups of stocked fish may become just as important.

Thesis outline and objectives

In an attempt to understand the causes and potential implications of variable growth rates and sizes on the potential recruitment of sturgeon cohorts, studies were developed to: 1) determine the mechanisms behind these observed variations and 2) assess the behavioural and physiological consequences of being either a fast- or slow-grower (i.e., large or small). To address these questions, both laboratory and field studies utilizing Lake Sturgeon were employed. Lake Sturgeon occupy the most northerly reaches of any sturgeon species, with the exception of Siberian sturgeon (Artyuklin 1995), and reside within the Great Lakes, Hudson-James Bay and Mississippi River watersheds (Pikitch et al. 2005). This species of sturgeon is among the latest to reach reproductive maturity (20 to 25 years for females and 12 to 15 years for males) and has relatively long intervals between spawning events (3 to 5 years for females and typically every other year for males; Bruch and Binkowski 2002; Pikitch et al. 2005). In an attempt to bolster low population numbers, stock enhancement programs are frequently implemented (Schram et al. 1999; Jackson et al. 2002; Auer 2004). As such, further knowledge regarding the factors contributing to recruitment success of Lake Sturgeon cohorts (both natural and artificial) would greatly assist in current and future decisions regarding their conservation.

In addressing the means of growth rate variability among sturgeon cohorts, Chapter 2 was dedicated to determining whether this observation is influenced more by extrinsic (e.g., environment) or inherent (e.g., genetic predisposition) mechanisms. Fashioned after the experiments conducted by Koebele (1985), larval Lake Sturgeon were

reared under three conditions: 1) individuals permanently isolated by opaque partitions, 2) individuals reared in groups and never separated, and 3) individuals separated by opaque partitions only when fed. Two additional factors that were incorporated into the study were family background and feeding rates. It was hypothesized that if growth rates are more heavily influenced by inherent factors, size variability among individuals reared in isolation would be equal to (or greater than) those individuals subjected to rearing environments allowing group interactions. It would also be expected that family background would have a greater influence on the final results than feeding rates. Alternatively, if growth rates are influenced more by extrinsic factors, it was hypothesized that size variability would be greater among individuals reared in groups than those individuals reared in isolation. Under this scenario, it would also be expected that feeding rate would have a greater bearing on final results than family background.

Group interactions during feeding events and feeding rate were determined to be the most influential factors leading to size variability over time and, as such, Chapter 3 was designed to address whether competitive asymmetries are a reflection of fixed behavioural phenotypes (Dall et al. 2004; Sih et al. 2004) or the result of competitive advantages associated with absolute size (Van Buskirk 1992; Post et al. 1999; Aljetlawi and Leonardsson 2002). Under the framework of an unequal competitors ideal free distribution (Sutherland and Parker 1985), the feeding interactions among size-matched fast- and slow-growers and relatively large and small cohort members were observed in aquaria set up to provide both good and poor foraging patches. It was hypothesized that if fast-growing and (or) large juvenile Lake Sturgeon were competitively superior to their slower-growing and smaller tank mates, the fast-growers and (or) large fish would spend

a greater than expected proportion of time in the good foraging patch.

In Chapter 4, research related to the physiological consequences of absolute size among Lake Sturgeon individuals, and its potential influence on recruitment, was conducted. The performance (e.g., survival, condition, endogenous energy reserves) of relatively large and small members of the same Lake Sturgeon cohort were recorded over the course of a prolonged temperature challenge. Absolute body size is known to play a significant role in the ability of young-of-the-year fish to survive over winter (Hurst and Conover 1998; Pangle et al. 2004) and, given the northern distribution of Lake Sturgeon populations combined with the tendency for fall stocking programs of this species, a prolonged low water temperature challenge is highly relevant for assessing potential recruitment. It was hypothesized that all individuals would be negatively affected following a drop in water temperature (e.g., mortality, reduced body condition) but that the smallest individuals would be more affected by these changes than the largest individuals.

Laboratory studies are highly useful for gaining information about variables in response to specific factors; however, this approach can never fully represent the myriad of conditions experienced within natural environments. Therefore, a large-scale field study was undertaken in conjunction with laboratory-based research. Hatchery-reared Lake Sturgeon were released into the Winnipeg River in the fall of their first year and during the spring as one year olds. It was hypothesized that if absolute size is the primary indicator of successful recruitment, as is most often implied, then the coefficient of variation (CV) for length and weight among recaptured individuals would be less than the CV values calculated prior to stocking following both release events. Furthermore, it was

predicted that under this assumption, recapture rates among the larger yearling Lake Sturgeon would be greater than for those individuals stocked out in the fall at 3 months of age.

The final chapter outlines the means and consequences of inter-individual differences in growth rate and size among juvenile Lake Sturgeon and offers potential implications for natural and artificial recruitment among year-classes. Several unexpected and novel outcomes emerged throughout the research program and a number of future research directions are put forward to improve future Lake Sturgeon recovery efforts.

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CHAPTER 2

Influence of inherent and extrinsic factors on the growth rate variability of
larval Lake Sturgeon

Abstract

Mechanisms generating inter-individual differences in growth rate within fish cohorts have been linked to both inherent (e.g., genetic) and extrinsic (e.g., environmental) factors. To determine which of these factors is more influential on growth rates among hatchery-reared Lake Sturgeon, *Acipenser fulvescens*, larvae were reared under three conditions: 1) individuals permanently isolated, 2) individuals reared in groups and 3) individuals isolated only during feeding events. It was hypothesized that if growth rates were influenced more by inherent factors, the coefficient of variation (CV) for total length among individuals reared in isolation would be equal to, or greater than, that determined for individuals subjected to rearing environments allowing group interactions. Mean CV values were found to be significantly greater among larvae reared in groups than for those individuals reared in isolation, and there was no significant difference between the mean CV values for fish permanently isolated and those that were isolated only when fed. These outcomes indicate that extrinsic factors had a greater influence on growth rate variability among larval Lake Sturgeon than inherent factors, and more specifically suggest that asymmetric competitive abilities during feeding events drive this phenomenon. Furthermore, reduced feeding rates amplified size divergence and this was assumed to be due to more intensive interactions during feeding events. It is unclear whether size alone determined the success of competitive outcomes or whether inter-individual differences in behaviour, physiology, or both contributed to asymmetric competitive abilities among Lake Sturgeon individuals.

Introduction

Growth variability among individuals of the same cohort, leading to quantifiable size differentiation, has long been observed in both cultured and wild fish species prompting much discussion about the possible mechanisms involved in creating such divergence (Brown 1946; Magnuson 1962; Huston and DeAngelis 1987; Pfister and Stevens 2002). Competitive asymmetry, particularly the formation of dominance hierarchies, is generally accepted as the primary contributor to growth variability. Dominance hierarchies can include aggressive interactions whereby dominant individuals physically impede food consumption by subordinates (Irwin et al. 2002; Hojesjo et al. 2004) or can be 'psychological' in nature, as a result of stress-induced growth rate reductions among subordinates (Abbott and Dill 1988; Montero et al. 2009). However, non-interactive mechanisms, most notably spatial and temporal heterogeneity, may play an even greater role in persistent size variability among individuals of the same cohort (Huston and DeAngelis 1987). Some examples of non-interactive mechanisms include unequal access to profitable habitats (Casten and Johnston 2008) or size-dependent diet shifts that amplify small initial size differences (Huss et al. 2008). Multiple spawning events within a single reproductive season are possible due to interruptions, most notably temperature fluctuations (Auer and Baker 2002), and have also been suggested as a potential non-interactive mechanism causing size heterogeneity within cohorts (Huston and DeAngelis 1987).

The mechanisms outlined above can be broadly classified as extrinsic factors, but an equally valid explanation for growth variability concerns inherent mechanisms (Huston and DeAngelis 1987). Assessing genetic variability among individuals requires

studies of heritability or studies where individuals can be compared while being reared in isolated, and similar, environments. Several studies using this latter technique, with a specific focus on growth rates, have been conducted with varying conclusions made as to the mechanisms involved. Wang et al. (1998) found that hybrid sunfish, *Lepomis cyanellus* x *L. macrochirus,* reared in isolation showed marked differences in daily food consumption, growth and gross growth efficiency (weight gain/cumulative consumption) suggesting inherent variation among individuals. Martins et al. (2005a,b) came to a similar conclusion for the African Catfish, *Clarias gariepinus*, in their studies looking at feed intake, feeding efficiency, feeding behaviour and growth. However, several experiments that have included group rearing treatments in addition to isolated rearing treatments, have come to different conclusions. When Koebele (1985) compared the growth rate variability among juvenile cichlids, *Tilapia zillii*, under isolated and group rearing, higher growth variability was observed among individuals reared together. This led the author to conclude that dominant-subordinate relationships among tank mates were more at play in the development of heterogeneous growth than inherent capacities. Likewise, juvenile Arctic Char, *Savelinus alpinus,* varied greatly in their ability to acquire food, resulting in higher growth rate variability when compared to individuals reared in isolation (Jobling and Baardvik 1994). Conflicting conclusions about the source of growth variability suggest that this phenomenon is not simply the result of a single mechanism but likely the result of both inherent and extrinsic factors influencing growth rate.

Intra-cohort growth variability continues to receive interest due to the many effects it can have at both an individual and population level. From an ecological

standpoint, high growth rates are often associated with individual fitness, particularly in north-temperate environments where overwinter survival depends on adequate body reserves (Cargnelli and Gross 1997; Biro et al. 2004a). Growth rates have been linked to differences in physiological demands (Peck et al. 2004) and risky foraging behaviours (Biro et al. 2004b). Such inter-individual differences within a cohort can affect how a population is able to respond or adapt to extrinsic factors, including resource depletion or predation pressure (Wilson 1998). In aquaculture, growth rate variability may influence production practices to maximize growth rates for all individuals (e.g., size-sorting).

Currently there is limited information about the mechanisms causing growth rate variability observed within wild (Peterson et al. 2000; Braaten and Fuller 2007) and cultured (Monaco et al. 1981; Nathanailides et al. 2002) juvenile sturgeon cohorts. Most sturgeon populations are under considerable threat (Peterson et al. 2007) and, as a result, are often supplemented with hatchery-reared individuals (Ireland et al. 2002; Jackson et al. 2002; Steffensen et al. 2010). Under these circumstances, intra-cohort variability must be understood from both an ecological and aquaculture perspective in order to effectively utilize stocking programs. The primary purpose of this research was to determine whether growth rate variability, consistently observed among hatchery-reared Lake Sturgeon, *Acipenser fulvescens*, was the product of inherent capacity or of extrinsic mechanisms (e.g., asymmetrical competitive ability). It was hypothesized that if growth rates are influenced more by genetics, size variability among individuals reared in isolation would be equal to (or greater than) individuals subjected to rearing environments allowing group interactions. The second objective of this study was to determine the influence that feeding level, social interaction and family group has on the above results.

Methods

Experimental animals

Larval Lake Sturgeon used in this study were the product of gametes collected from wild spawning adults captured in the Winnipeg River directly downstream of the Slave Falls (50°13'21N, 95°34'06W) and Pointe du Bois (50º17'52N, 95º32'51W) Generating Stations in the year 2008 and 2009, respectively. During both study years, experiments were conducted on multiple family groups. To facilitate the synchronization of egg fertilization and hatch using the eggs from multiple individuals, gravid females were injected with a commercially available hormonal agent (Ovaprim®, Syndel Laboratories Ltd., Vancouver, BC, Canada) known to induce ovulation in a number of fish species (Brzuska and Adamek 1999; Haniffa and Sridhar 2002; Hill et al. 2009) including Lake Sturgeon (C. Klassen, unpublished data). The total dose of hormone used per fish was based on body mass (0.5 ml/kg) with a priming injection (10% of total dose) followed by a second injection 12 hours later (90% of total dose).

Females selected as broodstock were maintained within a 600-gallon tank set up along the shore of the spawning grounds and no individual was captive for longer than 5 days. In 2008, eggs from three females and the milt from five different males created five genetically distinct families and in 2009, three genetically distinct families were produced with the eggs from three females and the milt from three males (Table 2.1). In both years, a genetically mixed group of larval sturgeon were produced by fertilizing the eggs from multiple females with the milt from multiple males collected in that year. In this way, the growth performance of larval Lake Sturgeon within each rearing treatment could be compared between families and measured against a group more representative of the population, as it is known that multiple males mate with a single female in the wild

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(Bruch and Binkowski 2002).

Egg incubation took place within McDonald hatching jars (round-bottomed, 13-L capacity cylinder, 0.5 m tall and 0.2 m in diameter) that were set up in a water re-circulation system built at the Canadian Rivers Institute Field Station (Pinawa, Manitoba, Canada) located approximately 35-40 km downstream of the natural spawning grounds. Water was collected directly from the Winnipeg River and transported to the field station at weekly intervals, where it was passed through a Rainfresh (Envirogard Products Limited, Richmond Hill, ON, Canada) coarse pore sediment cartridge (25-30 µm) prior to entering the system. Once in the re-circulation system, water ran continuously through a second coarse pore filter system and UV light sterilizer. Incubating eggs were maintained at temperatures of 12 ± 1 °C and kept out of direct sunlight. Eggs were exposed to overhead fluorescent lights for a maximum of 5 hours daily, during which time dead eggs and fungus were removed from the hatching jars.

Rearing conditions

Following hatch in 2008, yolk-sac larvae were transported to the Animal Holding Facility (AHF) at the University of Manitoba, Winnipeg, Manitoba, Canada. The study animals were maintained within a flow-through water system fed by de-chlorinated tap water. Florescent light bulbs were set on a timer to create a 12:12 h light:dark photoperiod. In 2009, yolk-sac larvae remained at the Canadian Rivers Institute Field Station for the duration of the study period and were subjected to the same water-recirculation system that was used during the hatching period. Fish were exposed to a 16:8 h light:dark photoperiod produced by both natural light entering from lab windows and overhead florescent light bulbs. Water temperatures were maintained at 15 ± 1 °C in

both locations. Live brine shrimp (*Artemia* spp.) nauplii (Argent Laboratories, Redmond, WA, USA) were fed to larval fish twice daily (morning and evening) with feeding events lasting approximately 1 hour. The water flow was turned off during feeding and was returned when all uneaten brine shrimp were removed from the experimental tanks.

Year 1: Group and isolated rearing at two feeding levels

To determine if growth rate variability among hatchery-reared individuals was the result of genetic inheritance or asymmetrical competitive abilities, custom experimental tanks were constructed using 6 mm thick polyvinyl chloride (PVC) sheets. Each tank measured 72 x 9 x 7 cm (L x W x H) and was partitioned in the center to create two equal rearing environments that measured 36 x 9 x 7 cm. On one side, seven opaque partitions were added at an equal distance generating eight 4.5 x 9 x 7 cm rearing compartments. On the other side, no partitions were added and the rearing environment remained open (Figure 2.1).

A maximum of eight experimental tanks were positioned in shallow fiberglass trays measuring 122 x 75 x 9 cm. Water was distributed at the upstream end and exited via a standpipe at the downstream end. Sixteen windows (covered by small mesh screen) were added along the front and back of each experimental tank to allow fresh water to flow evenly through the tanks (Figure 2.2).

Sixteen larval Lake Sturgeon, having a genetically mixed background, were arbitrarily selected and placed into experimental tanks one week following the start of exogenous feeding. Eight fish were placed together in the larger, open rearing environment (allowing group interactions) and 8 fish were placed individually into each one of the smaller rearing compartments (preventing group interaction). While the latter

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individuals were confined to a smaller space than their counterparts, this design maintained the fish per area ratio between Lake Sturgeon in each of the treatments. If a fish died in the interactive rearing environment, a partition was placed in the tank such that the number of fish per cm^3 remained constant. Each of the two treatments (i.e., group rearing and isolated rearing) were replicated four times. In addition, this procedure was repeated for each of the family groups used (A, B, C, D, and E).

It was unknown if the feeding level administered to experimental animals would have a bearing on the final growth rate variability observed among individuals reared in group and isolated environments. Therefore, the entire experimental design (described above) was repeated using two feeding levels, satiation and half satiation. A micropipette was used to maintain set feeding levels. In this way, the number of brine shrimp (suspended in 1 L of water) could, as best as possible, be equally allocated among the larval fish when drawing up and dispensing 1 and 0.5 ml suspension of brine shrimp per individual in the satiated and half satiated feeding treatments, respectively. Throughout this research, satiation was defined as the amount of brine shrimp necessary to have some remaining in the treatment tanks following a one-hour feeding event. The amount of brine shrimp delivered was adjusted throughout the study, as needed.

Comparisons among study animals maintained in the experimental treatments were carried out for growth rate variability, mean total length and final survival rate. Growth rate variability was quantified by determining the coefficient of variation (CV = standard deviation/mean) for total length measurements within each replicated experimental treatment. For example, the CV was calculated from the mean total length among the eight individuals placed in a group or isolated rearing treatment, respectively.

In order to obtain individual fish lengths at the start (July 3) and end (July 24) of the study, digital images (Canon PowerShot A60, Canon Canada Inc., Mississauga, ON, Canada) of each rearing tank were captured, and total lengths of individuals were determined using ImageJ (version 1.43, National Institutes of Health, Bethesda, Maryland, USA). For example, pictures were taken of each individual housed in the isolated chambers, while those individuals in group rearing environments were photographed from further away in order to capture the images of all fish in a treatment tank. A ruler placed next to the tank provided scale to measure fish length. It was later determined that slight distortions in these latter photographs caused the size variability to be overestimated in the group rearing environments (i.e., individuals positioned along the periphery of the photographs were measured as slightly shorter than they actually were). This issue was rectified in 2009 (see below).

The mean coefficient of variation values, mean total lengths and final survival rates were compared among treatments at the end of the study. Mean values were assessed for normality and equal variance using residual plots and Cochran's test, respectively (Underwood 1997). Survival rates were subjected to arcsine transformations prior to analysis. A three-way analysis of variance (ANOVA) where rearing environment, feeding level and family group represented fixed factors was followed with the Tukey-Kramer multiple-comparison test when differences among means were significant. Statistical computations were performed with the JMP® 8.0.1 statistical software package (SAS Institute Inc., Cary, NC, USA) and significant differences were accepted when $P \leq 0.05$ for this and subsequent analyses.

Year 2: Group and isolated rearing with allowance for social interactions

In 2009, the experimental design was identical, with three notable exceptions: 1) larval Lake Sturgeon were distributed within the experimental rearing treatments at the start of exogenous feeding, 2) only three family groups were tested (F, G, H), and 3) a third treatment was incorporated into the study to assess general interactions versus interactions specifically during feeding events. To clarify, the new treatment allowed the eight individuals within a group rearing treatment tank (e.g., 36 x 9 cm) to interact with one another throughout the entire study, with the exception of feeding events. Prior to feeding events, the seven partitions were positioned within the tank such that each larval sturgeon was confined to a space similar to that of the experimental animals permanently isolated (e.g., 4.5 x 9 cm). Uneaten brine shrimp were removed from each compartment prior to removal of the partitions post feeding. Throughout the course of this experiment, feeding levels were set at or near satiation for fish in all treatments.

Fish measurements (total length) were taken at the start (June 29) of the study and at weekly intervals thereafter until the end of the study (July 27). The CV for total length was calculated in the same way as described above with one notable difference. Each larval fish was removed from their treatment tank and placed in a small bowl of tank water prior to being photographed. This method ensured all fish could be centered in the frame and photographed from an equal distance.

The mean coefficient of variation values, mean total lengths and final survival rates were compared among treatments throughout the study. Variables were assessed for normality and equal variance using residual plots and Cochran's test, respectively (Underwood 1997). Survival rates were subjected to arcsine transformations prior to

analysis. A two-way analysis of variance (ANOVA) where rearing environment and family group represented fixed factors were followed with the Tukey-Kramer multiple-comparison test when differences among means were significant.

Results

Year 1: Group and isolated rearing at two feeding levels

At the start and end of the study in 2008, statistical analysis of size variability (CV) and total lengths using a three-way analysis of variance, respectively, revealed no significant interactions between rearing environments (group, isolated), feeding levels (satiation, half satiation) and family groups tested (A, B, C, D, E, MIX; Table 2.2). In addition, no significant interactions were present between rearing environment and feeding level (independent of family group), rearing environment and family group (independent of feeding level), and family group with feeding level (independent of rearing environment; Table 2.2). As such, the three fixed factors were assessed independently from one another.

Prior to experimentation, no significant differences in CV values (i.e., size variability) were present among fish distributed among the two feeding treatments, although significant differences in CV were present among the genetically distinct family groups used (Table 2.2; Figure 2.3). Unexpectedly, there were significant differences in CV among the fish distributed in the two rearing environments at Week 0 (Table 2.2; Figure 2.3); however, this result is believed to be the product of the measuring inaccuracy described above.

Mean total length between fish allocated to the two rearing environments and feeding levels were not significantly different at Week 0 (Table 2.2; Figure 2.4).

However, the mean total length of Family 'D' was found to be significantly greater than the other family groups tested at the start of the study (Table 2.2; Figure 2.4).

At the end of the three week study, statistical analysis of CV for total length indicated that larval sturgeon reared in group environments were significantly more variable in their sizes than those individuals maintained in isolation (Table 2.2; Figure 2.3). While it is difficult to determine the effect rearing environment had on variable growth rates due to the fact significant differences were already present from the start of the experiment, it is important to note that CV values increased significantly over time for individuals in group environments (paired t-test; $t = -2.39$, $df = 47$, $P = 0.021$) while CV values significantly decreased over the same period of time for individuals in an isolated environment ($t = 2.45$, $df = 47$, $P = 0.018$; Figure 2.3). In contrast to the initial assessment, family groups did not differ significantly in their size variability at the end of the study (Table 2.2; Figure 2.3). Interestingly, larval sturgeon fed to half satiation had significantly higher size variability than those individuals fed to complete satiation during the study (Table 2.2; Figure 2.3).

With respect to mean total lengths, analysis showed that there was no significant difference between individuals reared in the two environments over the course of the study, but highly significant differences in mean length between individuals fed to satiation versus half-satiation and among larval fish having different genetic backgrounds (Table 2.2; Figure 2.4).

The mean final survival of larval sturgeon within the treatments tested in 2008 was analysed with a 3-way ANOVA which did not produce significant interactions between rearing environment, feeding levels and family groups (Table 2.2). No

interactions were present between rearing environment and feeding level (independent of

family group), rearing environment and family group (independent of feeding level) or,

family group with feeding level (independent of rearing treatment; Table 2.2). The

overall mean (±SE) survival was high following the three week study at 89 ± 1.5%.

Mean final survival was not significantly different among individuals fed to satiation and

half-satiation (Table 2.2; Figure 2.5); however, larval sturgeon reared in isolated

chambers had significantly lower survival than those individuals reared in group

environments (Table 2.2; Figure 2.5). There were also significant differences in the rate

of survival among fish from the different genetic backgrounds (Table 2.2; Figure 2.5).

Year 2: Group and isolated rearing with allowance for social interactions

A two-way analysis of variance did not reveal any significant interactions

between rearing environment (group, permanently isolated, isolated at feeding events)

and family group (F, G, H, MIX) in Weeks 0, 1, 2, 3 or 4 of the 2009 study when

assessing CV (i.e., size variability) and mean total length, respectively (Table 2.3). As

such, results among rearing environments and family groups are presented independently

of each other.

At the point of exogenous feeding, there were no significant differences in size

variability among fish selected to be in the three rearing treatments nor were there any

statistical differences among the four family groups included in this study (Table 2.3;

Figure 2.6). This outcome persisted one week into the study for larval sturgeon in all

rearing environments and for all family groups (Table 2.2; Figure 2.6). In fact, significant

differences in CV values among family groups were not detected at any point in the study

(Table 2.3; Figure 2.6). However, this was not the case for larval sturgeon held in the

different rearing environments. Two weeks into the study, larval sturgeon maintained in permanent isolation were significantly less variable in their sizes than either those individuals reared in groups or isolated exclusively at feeding events (Table 2.3; Figure 2.6). Following an additional week in their designated rearing treatments, size variability was significantly lower among individuals permanently isolated, as well as isolated exclusively at feeding events, when compared to those individuals allowed to live in group environments permanently (Table 2.3; Figure 2.6). This was the same outcome at the end of the four-week study (Table 2.3; Figure 2.6).

In assessing the mean length of individuals, there were no significant differences among individuals placed in the three rearing treatments at the start of the study (Table 2.3; Figure 2.7). However, significant differences were detected among the family groups during each week (Table 2.3; Figure 2.7). For example, larval Lake Sturgeon of Family 'F' were consistently smaller than individuals from the other family groups, with the exception of week 0 (Figure 2.7).

Over the course of the study, mean length for sturgeon maintained in the three rearing environments showed similar trends to the results seen for the CV values (Figures 2.6 and 2.7). Following one week in permanent isolation, larval sturgeon had significantly lower mean total lengths than those individuals isolated during feeding time or kept in group environments continuously (Table 2.3; Figure 2.7). By Week 2, individuals in group rearing environments were significantly larger than fish reared in both permanently and non-permanently isolated chambers and this outcome continued until the end of the four week study (Table 2.3; Figure 2.7).

The overall mean (±SE) survival in the 2009 study was 88 ± 2%. Statistical

analysis did not produce significant interactions between rearing environment and family groups when applying a two-way analysis of variance (Table 2.3; Figure 2.8). In contrast to the 2008 study, mean final survival rates were not significantly different among fish reared in the three different environments but were significantly different among the family groups (Table 2.3; Figure 2.8).

Discussion

The primary purpose of this research was to determine whether growth rate variability, determined from observed size divergences, among hatchery-reared Lake Sturgeon, was influenced more by inherent factors or the surrounding environment (i.e., group interactions). Results from the 2009 study were similar to those from the 2008 study and together showed that larval sturgeon reared in group environments had greater variability in final total lengths than individuals reared in isolated chambers. The literature has suggested both inherent (Wang et al. 1998; Martins et al. 2005a,b) and extrinsic (Koebele 1985; Jobling and Baardvik 1994) mechanisms to explain growth rate variability among a number of fish species. Growth rates during early development in Lake Sturgeon appear to further support the latter explanation. However, through the examination of how feeding level, social interaction and family background influence the growth rates of larval sturgeon, the final mechanisms for producing growth rate variability in this study may not be so clear cut.

Feeding level played a significant role in the growth rate variability observed across treatments. Larval Lake Sturgeon reared under a low feeding regime (i.e., half satiation) had significantly higher variability in total lengths than those individuals reared under a high feeding regime (i.e., satiation). This result is similar to the study conducted

by Ewa-Oboho and Enyenihi (1999) where they found that reduced food availability was the most important factor affecting size variation in hatchery-reared African Catfish, *Heterobranchus longifilis*. Their study focused only on group rearing treatments and the authors speculated that small initial size variation allowed the larger fish to consistently consume greater amounts of food, which, in turn, led to greater size divergence through asymmetrical competitive abilities. Interestingly, Koebele (1985) had the opposite outcome when rearing juvenile cichlids in group environments having nearly unlimited access to food in comparison to groups reared under a restricted feeding regime. The author concluded that dominant individuals were still able to defend and consume a greater proportion of the food supply than the subordinates when reared together within a high resource environment. Highly aggressive and submissive behaviours were not observed in the current study and, as such, the competitive asymmetries observed may be more closely in line with those suggested by Ewa-Oboho and Enyenihi (1999).

A number of studies have been able to show strong correlations between initial egg size and emerging larval lengths (Ojanguren et al. 1996; Jardine and Litvak 2003; Paulsen et al. 2009), including Siberian Sturgeon, *A. baeri* (Gisbert et al 2000). This study did not examine such correlations, but all treatment tanks contained some initial variability among sturgeon with respect to total lengths (CV range: 0.02 to 0.08). Therefore, it is plausible that initially larger individuals in each of the group environments had a feeding advantage. This advantage cannot be attributed to diet shifts among larger individuals, as it was for young-of-the-year (YOY) Perch, *Perca fluviatilis* (Huss et al. 2008), because the sturgeon in this study were offered a single food source of uniform size (i.e., brine shrimp nauplii). The advantage of being larger in the current

experimental set-up would be limited to an increased ability to acquire resources and, subsequently, the overall number of brine shrimp consumed. Martins et al. (2005a,b) reported that larger African Catfish, *C. gariepinus*, were both faster eaters and more efficient in utilizing the energy in their feed than smaller conspecifics. The latter explanation can be ruled out in our experiment, because equally high size variations would have been observed among sturgeon reared in the isolated chambers (i.e., an inherent trait). However, the notion that the larger sturgeon were better able to respond to feeding events and therefore acquire a greater proportion of a limited food supply in the group rearing treatments, a phenomenon also observed in juvenile Arctic Char (Benhaim et al. 2003) and turbot, *Scophthalmus maximus* (Irwin et al. 2002), is still a plausible explanation for the observed size variability in this study.

The discrepancies observed among individuals reared in group and isolated environments could also be explained by taking a closer look at the latter treatment. For instance, it could be hypothesized that conditions in the isolated chambers created negative growing conditions (e.g., space constrictions) leading to homogenous growth. This hypothesis was not supported in 2008, as mean growth was not significantly different between experimental animals reared in small rearing compartments (i.e., isolated) and open rearing tanks (i.e., grouped). Although, survival was slightly compromised among fish reared in isolation and if consistently smaller (or consistently larger) individuals were removed from this treatment final size variability would be reduced. Interestingly, in 2009 the final survivals were not significantly different between treatments, but final mean lengths were significantly reduced among fish in isolated rearing treatments. In either case, these results suggest that fish reared in isolation were at

a slight disadvantage (either in growth or survival), which may have contributed to the lack of size variability. Additionally, it is possible that the isolated sturgeon in our experiment were experiencing some stress, an occurrence reported for isolated juvenile Lake Sturgeon originating from the same population as was used in this study (Allen et al. 2009). Furthermore, acute stress events have been correlated with reduced growth rates in Atlantic Salmon, *Salmo salar*, parr (McCormick et al. 1998) and, more recently, Pankhurst et al. (2008) found that a similar response was produced in immature Rainbow Trout, *Oncorhynchus mykiss*, when placed in confinement. These outcomes suggest that the lower survivals (in 2008) and growth rates (in 2009) among permanently isolated individuals may be attributed to a chronic state of stress experienced among fish reared within this environment, ultimately leading to size homogeneity.

It is also important to consider the results observed among individuals reared in the non-permanent isolated rearing treatment of 2009 to further understand the basis of growth rate variability among larval sturgeon. Under this rearing treatment individuals were not permanently isolated in a confined space, and were not subjected to potential competitive interactions during feeding events. Larval sturgeon maintained in this rearing treatment produced results that were similar to those generated by fish reared in permanent isolation. This indicates that the size variability observed in group environments may not be the result of 'psychological' stress imposed on subordinates by more dominant individuals, as this effect has been known to persist within subordinates even when they are allowed to feed independent of dominant individuals (Abbott and Dill 1988).

Results from the combined studies in 2008 and 2009 appear to support the

disproportional food acquisition hypothesis (Magnuson 1962), most likely due to initial

size differences that become amplified over time due to greater feeding rates by the larger

individuals and (or) higher activity rates among the larger individuals that lead to higher

feeding rates among these individuals. Qian et al. (2002) studied juvenile Chinese

Sturgeon, *A. sinensis*, of differing sizes with respect to food intake and activity levels.

Their results indicated that growth rates were positively related to food intake, mediated

by activity levels (i.e., distance moved and time spent swimming per day). In this sense,

the current study may have come full circle to indicate that inherent factors including

genetic predispositions (e.g., activity rates) or maternal effects (e.g., egg size) may play a

greater role than would be suggested if just basing conclusions on the results of the group

and isolated treatments alone. For example, the inherent effects may not have an

opportunity to be manifested among individuals reared in isolation and may indicate that

inherent capacities for growth are further influenced by the environmental situation,

another explanation for the discrepancies seen in previous studies of growth variability.

Finally, this study examined the influence of family background on growth

variability. Initially it was hypothesized that larval sturgeon from similar parentage would

have lower variability in lengths than individuals comprised of a mixed genetic

background. Ojanguren et al. (1996) reported a two- to three-fold increase in CV (length)

for mixed family groups than for sibling groups. This was not the case in the current

study. Although, interestingly, the CV (length) for genetically mixed groups of fish were

among the most variable early and yet among the least variable at the end of

experimentation in both study years. It is unclear why this occurred, as final sizes and

survival did not appear to be compromised for these groups in either year. High growth

variability within sibling groups has been reported (Nathanalilides et al. 2002) and prompts discussion of the possible fitness advantages that offspring variability may have from the perspective of parents, particularly if certain sizes of offspring are known to excel under different situations (e.g., limited resources, predation pressures).

In summary, the larval Lake Sturgeon in this study had greater size variability (total length) when reared in group environments than when reared in isolation. Thus, it is suggested that growth rate variability in Lake Sturgeon is mediated more through extrinsic factors (e.g., group interactions) than inherent mechanisms. Further study indicated that it was solely group interactions during feeding events that generated the observed size variability. While it remains unclear why some individuals consistently gained an advantage over others to create these size discrepancies, it is hypothesized that some of the individuals in each group rearing environment were better able to acquire resources due to quicker feeding responses (e.g., higher activity rates) or initial size advantages (e.g., maternal effects). Future studies on this species should focus on individual performances within group rearing environments over time to elucidate more precisely the mechanism producing the observed growth rate differences. In addition, the consistency of individual performances across a variety of environments may give further insight into potential links between offspring variability and fitness advantages.

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Table 2.1 Summary of family relatedness and maternal measurements. Information that was not available is represented by n/a.

Year	Family	Female x Male	Fork Length (mm)	Total Length (mm)	Weight (kg)
2008	A	1 x 1	1360	1490	n/a
	B	2 x 2	1175	1296	n/a
	C	1 x 3	1360	1490	n/a
	D	3 x 4	1395	1510	n/a
	E	2 x 5	1175	1296	n/a
2009	F	4 x 6	1140	1268	14
	G	5 x 7	963	1067	8
	H	6 x 8	1455	n/a	26

Table 2.2 Results of a three-way analysis of variance comparing size variability (coefficient of variation, CV), total length and final survival among larval Lake Sturgeon from six different family backgrounds subjected to two rearing environments (isolated, grouped) at two feeding levels (satiation, half-satiation), respectively. Values were assessed at the start (Week 0) and end (Week 3) of the study. Analysis of final survival was not applicable (n/a) during Week 0.

Source	CV (Total Length)	Total Length (mm)	Final Survival (%)
Week 0			
Rearing Environment	$F_{(1,72)} = 5.97, P = 0.02*$	$F_{(1,72)} = 0.71, P = 0.40$	n/a
Feeding Level	$F_{(1,72)} = 1.29, P = 0.26$	$F_{(1,72)} = 0.64, P = 0.43$	n/a
Family Group	$F_{(5,72)} = 6.65, P = 0.01*$	$F_{(5,72)} = 4.67, P < 0.01*$	n/a
Rearing Environment x Feeding Level	$F_{(1,72)} = 0.64, P = 0.43$	$F_{(1,72)} = 0.73, P = 0.40$	n/a
Rearing Environment x Family Group	$F_{(5,72)} = 0.56, P = 0.73$	$F_{(5,72)} = 0.72, P = 0.61$	n/a
Family Group x Feeding Level	$F_{(5,72)} = 0.17, P = 0.97$	$F_{(5,72)} = 1.01, P = 0.42$	n/a
Rearing Environment x Feeding Level x Family Group	$F_{(5,72)} = 0.54, P = 0.74$	$F_{(5,72)} = 0.57, P = 0.73$	n/a
Week 3			
Rearing Environment	$F_{(1,72)} = 29.49, P < 0.01*$	$F_{(1,72)} = 1.25, P = 0.27$	$F_{(1,72)} = 24.34, P < 0.001*$
Feeding Level	$F_{(1,72)} = 6.13, P = 0.02*$	$F_{(1,72)} = 414.76, P < 0.001*$	$F_{(1,72)} = 0.09, P = 0.76$
Family Group	$F_{(5,72)} = 0.81, P = 0.55$	$F_{(5,72)} = 10.21, P < 0.001*$	$F_{(5,72)} = 3.69, P < 0.01*$
Rearing Environment x Feeding Level	$F_{(1,72)} = 2.07, P = 0.15$	$F_{(1,72)} = 1.26, P = 0.26$	$F_{(1,72)} = 1.08, P = 0.30$
Rearing Environment x Family Group	$F_{(5,72)} = 1.06, P = 0.39$	$F_{(5,72)} = 0.90, P = 0.49$	$F_{(5,72)} = 0.09, P = 0.99$
Family Group x Feeding Level	$F_{(5,72)} = 0.15, P = 0.98$	$F_{(5,72)} = 1.47, P = 0.21$	$F_{(5,72)} = 1.83, P = 0.12$
Rearing Environment x Feeding Level x Family Group	$F_{(5,72)} = 0.89, P = 0.49$	$F_{(5,72)} = 2.01, P = 0.08$	$F_{(5,72)} = 0.70, P = 0.62$

* Significant differences at $P \leq 0.05$

Table 2.3 Results of a two-way analysis of variance comparing size variability (coefficient of variation, CV), total length and final survival among larval Lake Sturgeon from four different family backgrounds subjected to three rearing environments (isolated, group, isolated during feeding events), respectively. Values were assessed at the initiation of the study (Week 0) and at weekly intervals until the end of the study (Week 4). Analysis of final survival was not applicable (n/a) during Weeks 0, 1, 2 and 3.

Source	CV (Total Length)	Total Length (mm)	Final Survival (%)
Week 0			
Rearing Environment	$F_{(2,36)} = 0.92, P = 0.41$	$F_{(2,36)} = 0.39, P = 0.68$	n/a
Family Group	$F_{(3,36)} = 2.69, P = 0.06$	$F_{(3,36)} = 8.11, P < 0.001^*$	n/a
Rearing Environment x Family Group	$F_{(6,36)} = 0.99, P = 0.12$	$F_{(6,36)} = 0.34, P = 0.91$	n/a
Week 1			
Rearing Environment	$F_{(2,36)} = 2.75, P = 0.08$	$F_{(2,36)} = 10.31, P < 0.001^*$	n/a
Family Group	$F_{(3,36)} = 2.52, P = 0.07$	$F_{(3,36)} = 40.64, P < 0.001^*$	n/a
Rearing Environment x Family Group	$F_{(6,36)} = 0.40, P = 0.87$	$F_{(6,36)} = 0.39, P = 0.88$	n/a
Week 2			
Rearing Environment	$F_{(2,36)} = 4.65, P = 0.02^*$	$F_{(2,36)} = 15.86, P < 0.001^*$	n/a
Family Group	$F_{(3,36)} = 1.53, P = 0.22$	$F_{(2,36)} = 25.84, P < 0.001^*$	n/a
Rearing Environment x Family Group	$F_{(6,36)} = 1.25, P = 0.30$	$F_{(6,36)} = 0.77, P = 0.60$	n/a
Week 3			
Rearing Environment	$F_{(2,36)} = 4.79, P = 0.01^*$	$F_{(2,36)} = 39.52, P < 0.001^*$	n/a
Family Group	$F_{(3,36)} = 1.82, P = 0.16$	$F_{(3,36)} = 47.70, P < 0.001^*$	n/a
Rearing Environment x Family Group	$F_{(6,36)} = 0.61, P = 0.72$	$F_{(6,36)} = 0.56, P = 0.76$	n/a
Week 4			
Rearing Environment	$F_{(2,36)} = 22.66, P < 0.001^*$	$F_{(2,36)} = 30.65, P < 0.001^*$	$F_{(2,36)} = 1.09, P = 0.35$
Family Group	$F_{(3,36)} = 2.75, P = 0.06$	$F_{(3,36)} = 27.62, P < 0.001^*$	$F_{(3,36)} = 5.87, P < 0.01^*$
Rearing Environment x Family Group	$F_{(6,36)} = 0.85, P = 0.54$	$F_{(6,36)} = 0.74, P = 0.62$	$F_{(6,36)} = 1.46, P = 0.22$

* Significant differences at $P \leq 0.05$
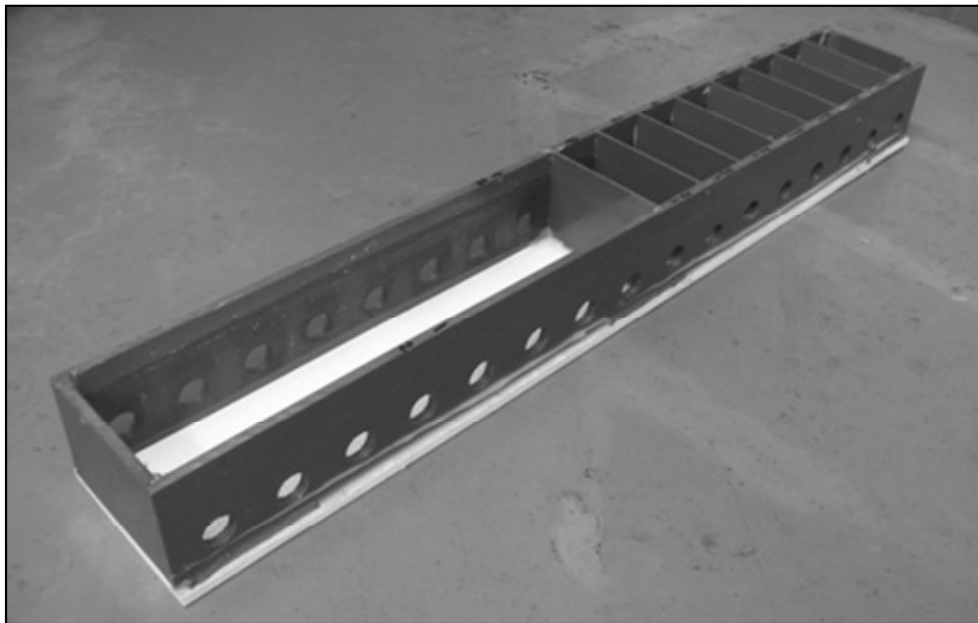
Figure 2.1 Custom-built experimental tank showing the group (left) and isolated (right) rearing environments. Eight larval Lake Sturgeon were placed into each of the rearing environments.

Figure 2.2 Laboratory set-up showing experimental tanks positioned in larger trays. Water was introduced at one end of the tray, passed through experimental tanks and exited a standpipe located at the opposite end.
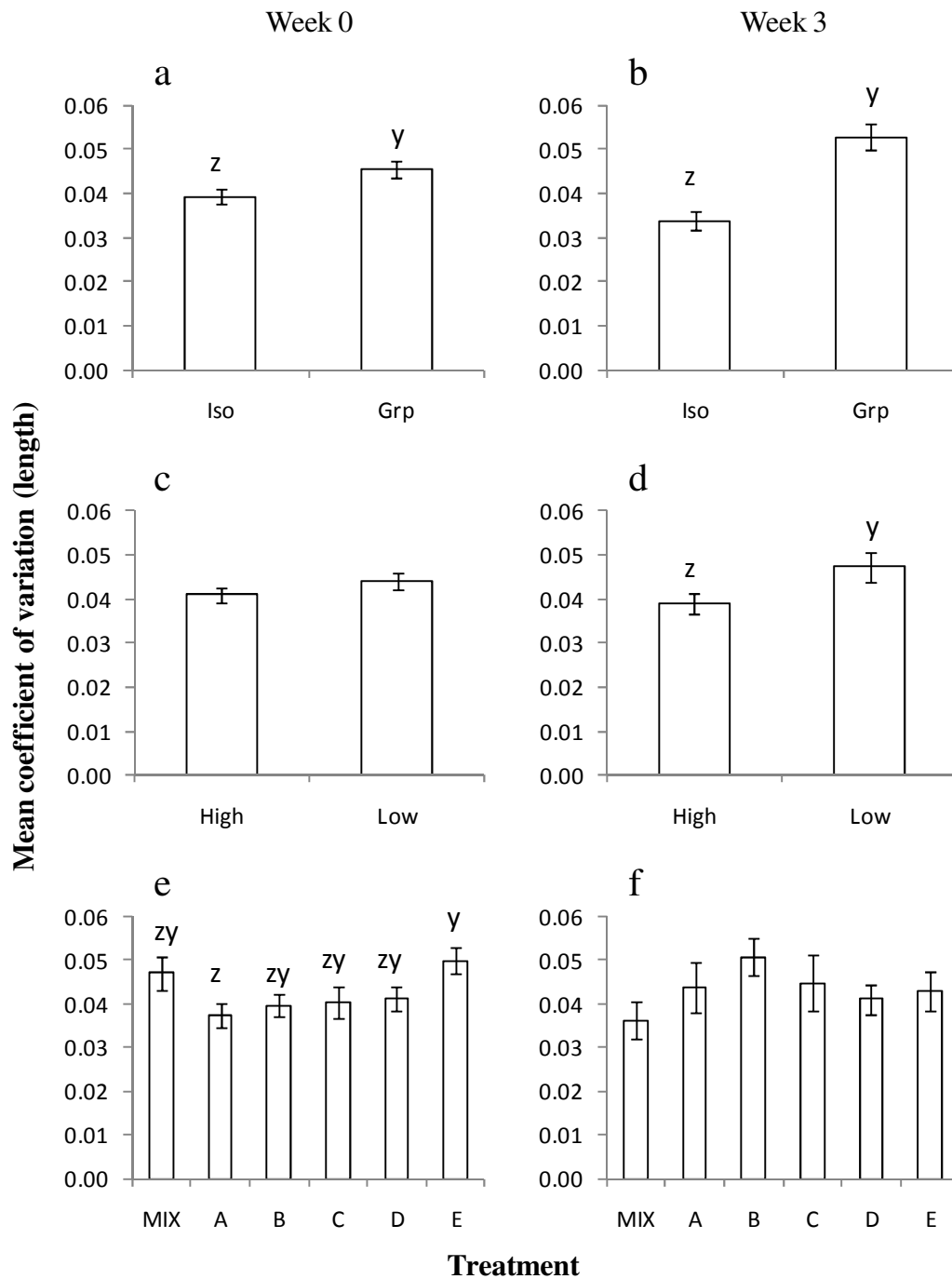
Figure 2.3 Mean coefficient of variation (CV) for length (± SE) of larval lake sturgeon in 2008 subjected to different rearing environments (isolated and group rearing, n = 48; a,b), feeding levels (high and low, n = 48; c,d) and having different genetic backgrounds (n = 16; e,f). The study commenced 1 week following the start of exogenous feeding and continued for a 3 week period. Different letters indicate significant differences at $P \leq 0.05$.
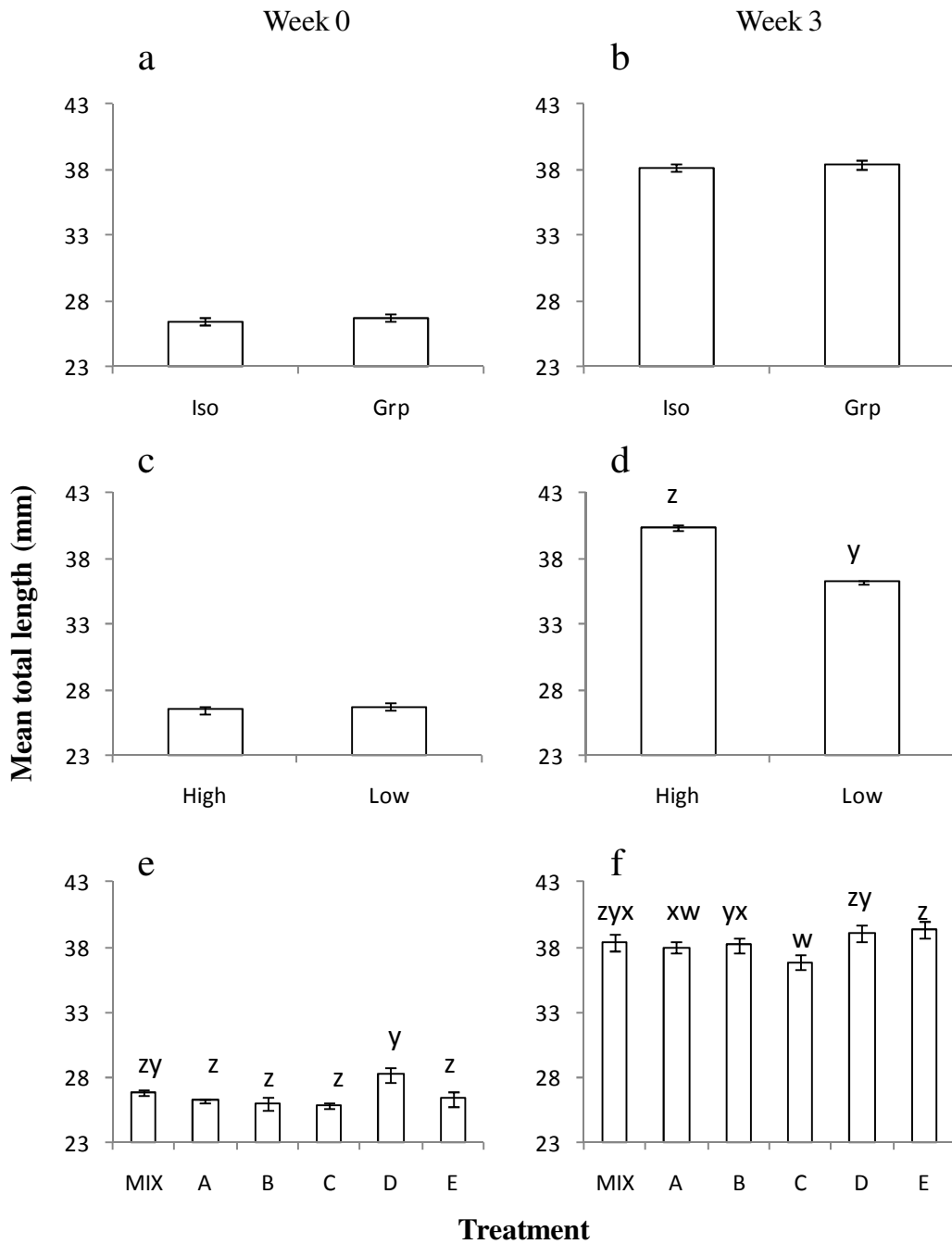
Figure 2.4 Mean length (± SE) of larval lake sturgeon in 2008 subjected to different rearing environments (isolated and group rearing, n = 48; a,b), feeding levels (high and low, n = 48; c,d) and having different genetic backgrounds (n = 16; e,f). The study commenced 1 week following the start of exogenous feeding and continued for a 3 week period. Different letters indicate significant differences at P ≤ 0.05.
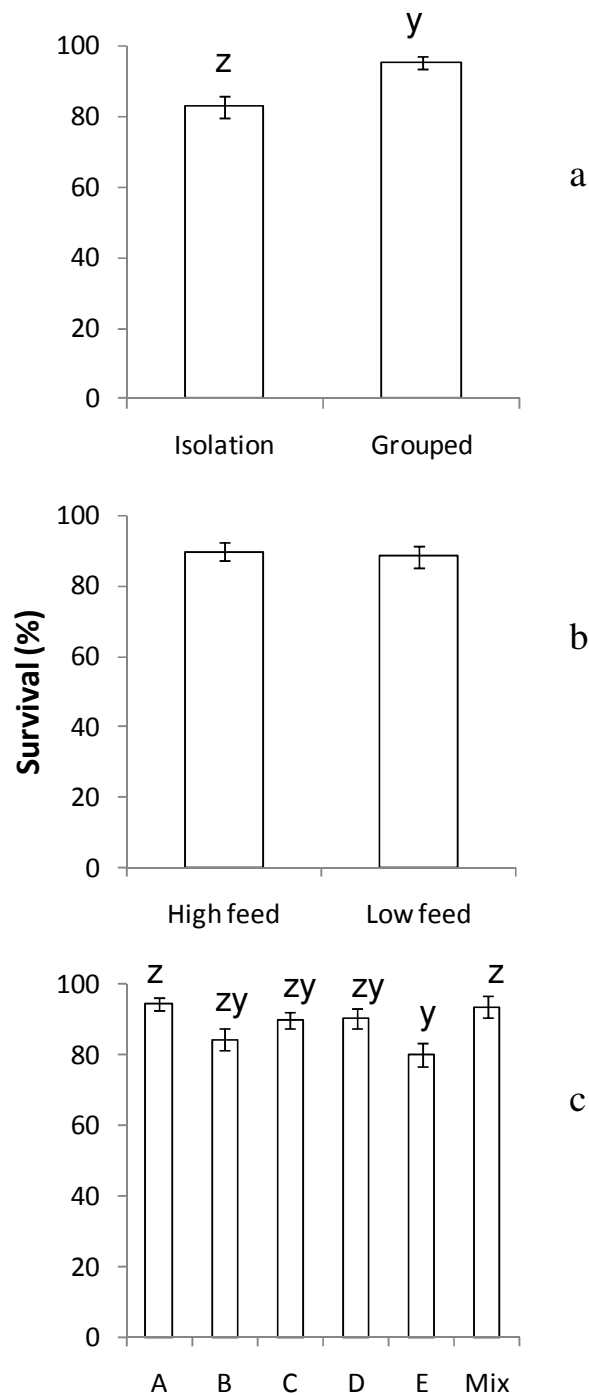
Figure 2.5 Mean final survival (± SE) of larval lake sturgeon in 2008 subjected to different rearing environments (isolated and group rearing, n = 48; a), feeding levels (high and low, n = 48; b) and having different genetic backgrounds (n = 16; c). The study commenced 1 week following the start of exogenous feeding and continued for a 3 week period. Different letters indicate significant differences at P ≤ 0.05.
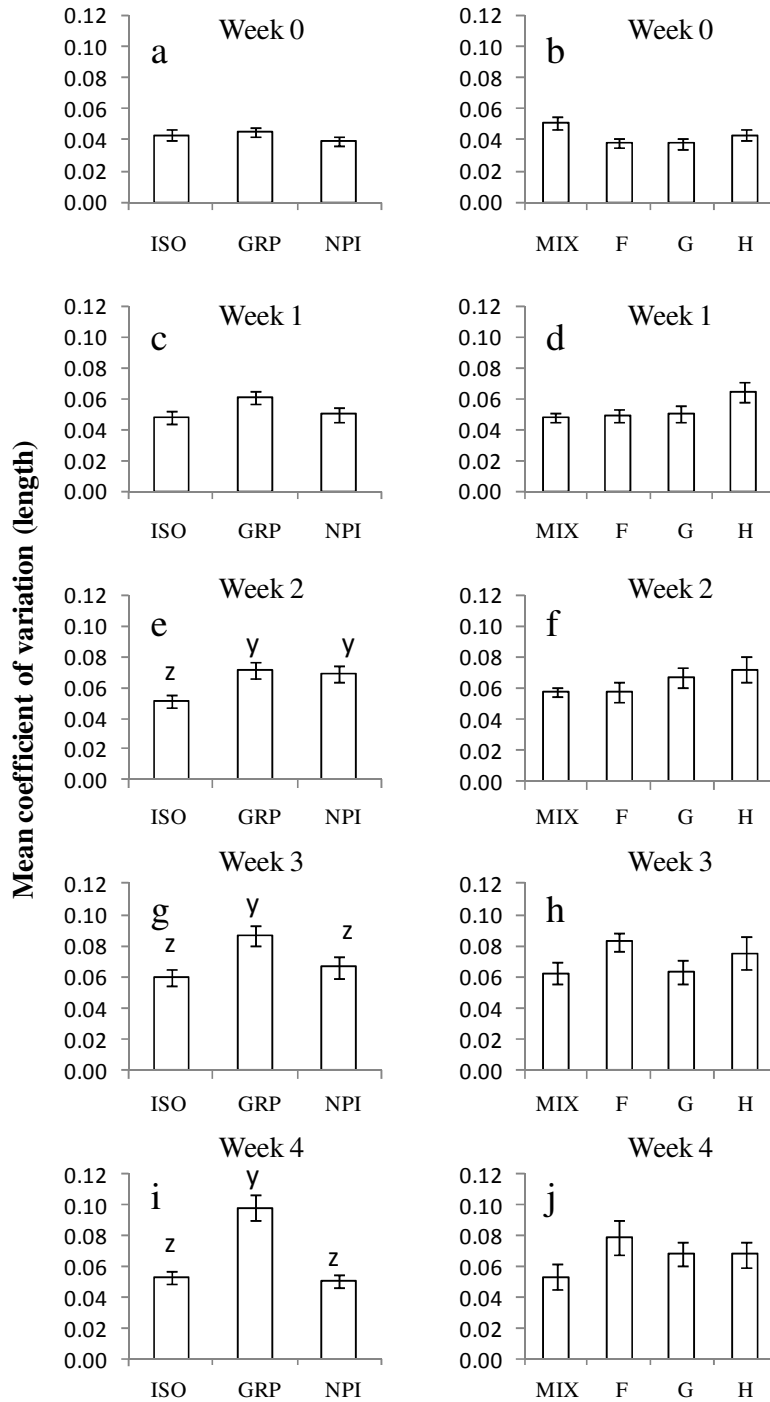
Figure 2.6 Mean CV (± SE) of larval Lake Sturgeon in 2009 subjected to different rearing environments (permanent isolation (ISO), group rearing (GRP) and non-permanent isolation (NPI), n = 16) and having different genetic backgrounds (n = 12). The study commenced at the start of exogenous feeding and continued for a 4 week period. Different letters indicate significant differences at P ≤ 0.05.
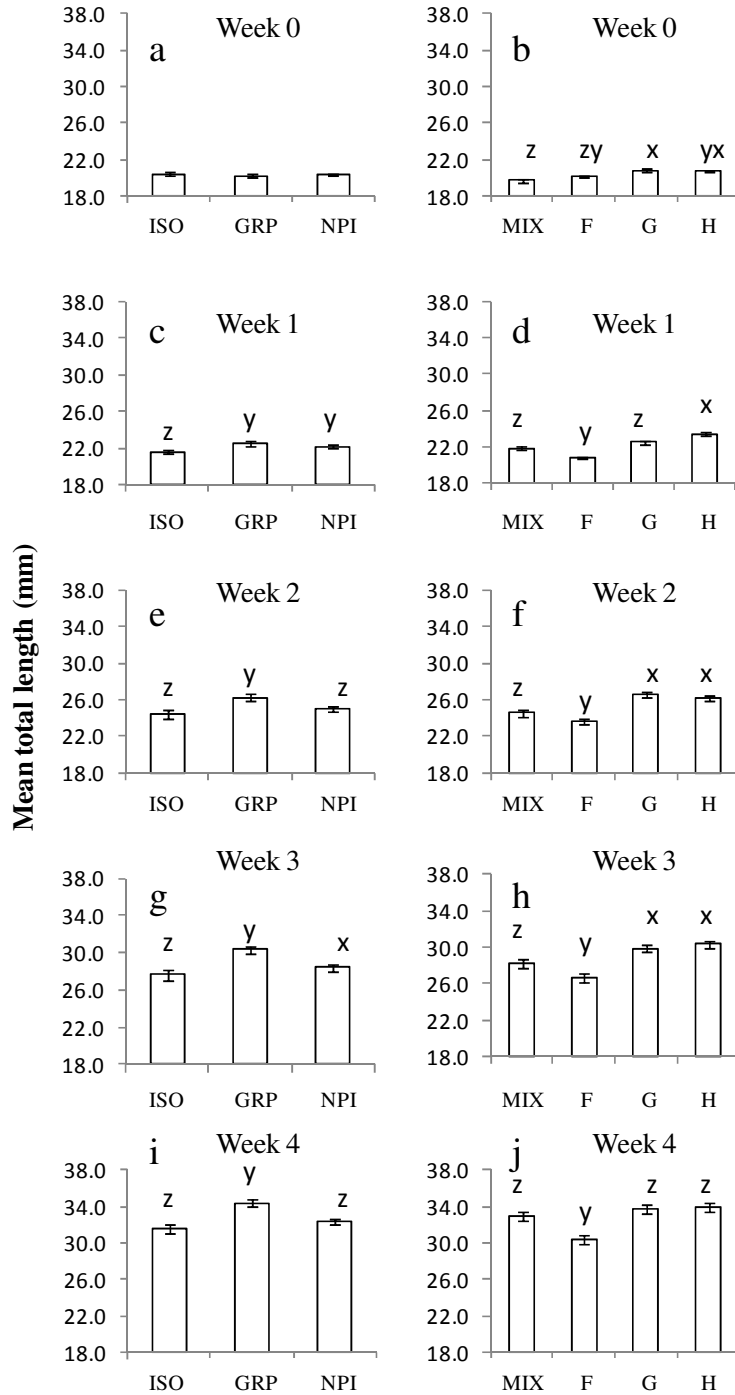
Figure 2.7 Mean length (± SE) of larval Lake Sturgeon in 2009 subjected to different rearing environments (permanent isolation (ISO), group rearing (GRP) and non-permanent isolation (NPI), n = 16) and having different genetic backgrounds (n = 12). The study commenced at the start of exogenous feeding and continued for a 4 week period. Different letters indicate significant differences at P ≤ 0.05.
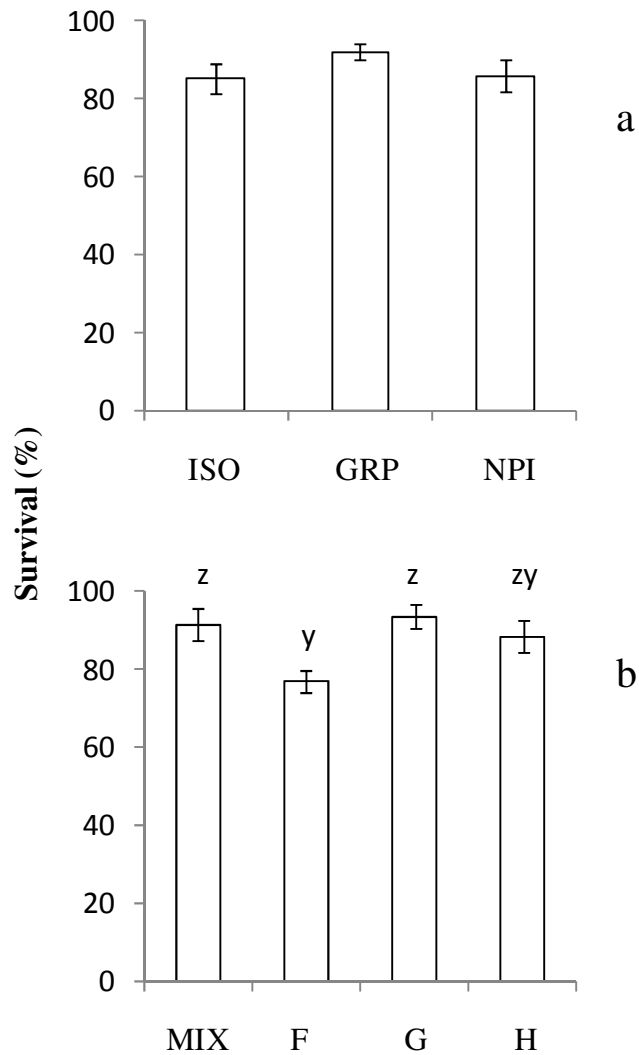
Figure 2.8   Mean final survival (± SE) of larval Lake Sturgeon in 2009 subjected to different rearing environments (permanent isolation (ISO), group rearing (GRP) and non-permanent isolation (NPI), n = 16) and having different genetic backgrounds (n = 12). The study commenced at the start of exogenous feeding and continued for a 4 week period. Different letters indicate significant differences at P ≤ 0.05.

CHAPTER 3

Competitive asymmetries among juvenile Lake Sturgeon during feeding
interactions: size-independent versus size-dependent factors

Abstract

Under culture conditions, Lake Sturgeon juveniles consistently display growth rate variability often leading to great size divergence within cohorts. The cause has been linked to group interactions during feeding events; however, it remains unknown whether successful food acquisition among Lake Sturgeon individuals is influenced more by size-dependent or size-independent factors. As such, the primary objective of this study was to determine if absolute size or an underlying behavioural phenotype best explain competitive asymmetries using the framework of an unequal competitors ideal free distribution. Studies utilizing aquaria with good and poor foraging patches (i.e., feed distributed 2:1) indicated that neither relatively large (i.e., size-dependent) or previously fast-growing but size-matched (i.e., size-independent) individuals monopolized the good foraging patch. In experiments quantifying the potential role of size-dependent and size-independent factors on foraging behavior, the activity choices of interacting groups were similar with no detected differences in the rate of patch-switching during feeding events. Therefore, the results of this study did not decisively reveal competitive superiority of any one group over another. It may be that experimental fish were unable to detect the different resource levels in the current experimental set-up and future study attempts should consider alternative study designs that can better accommodate the food searching behaviour of sturgeon.

Introduction

Persistent size differentiation within cohorts, most often mediated through inter-individual differences in growth rate, has been observed among plant and animal species (Pfister and Stevens 2002). A number of mechanisms contributing to this phenomenon have been suggested and can be broadly classified into either inherent or extrinsic factors. Among fish species, inherent mechanisms have included inter-individual differences in metabolic rates (Peck et al. 2004) and feeding efficiencies (Persson et al. 1998; Martins et al. 2005). Alternatively, competitive and social interactions between cohort members are examples of extrinsic factors and can produce variable growth rates through disproportional food acquisition (Keobele 1985; Gregory and Wood 1998; Irwin et al. 2002) or 'psychological' stress (Abbott and Dill 1988). Sturgeon species are also known to display inter-individual differences in growth rate variability under culture conditions (Monaco et al. 1981; Nathanailides et al. 2002; Qian et al. 2002), including Lake Sturgeon, *Acipenser fulvescens* (see Chapter 2). Recent study has indicated that the driving force behind these observations in hatchery-reared Lake Sturgeon are group interactions during feeding events (see Chapter 2), and suggests competitive asymmetries among cohort members. It remains unknown, however, whether successful food acquisition among Lake Sturgeon individuals is influenced more by size-dependent or size-independent factors.

Consumers can interfere with competitors passively by depleting resources prior to the arrival of others (exploitative), beat detected competitors to a food source (scramble), or aggressively challenge the presence of others (contest) (Ward et al. 2006). Generally, it is found that larger body sizes give competing fish an upper hand in

acquiring resources over smaller conspecifics (Post et al. 1999). However, competitive asymmetries may also reflect different behavioural phenotypes, also termed behavioural syndromes, that are size-independent (Sih et al. 2004; Reale et al. 2007; Stamps 2007). It is important to quantify both size-dependent and size-independent factors as Ward et al. (2006) pointed out that studies on competitive ability and body size may present cause and effect arguments. For example, are individuals good competitors because they are large or large because they possess superior competitive abilities?

Despite the gregarious nature of sturgeon species, only a few studies have attempted to quantify feeding interactions among individuals (Sbikin and Budayev 1991; Kynard and Horgan 2002; Allen et al. 2009), and it remains unclear if absolute size or potential underlying behavioural phenotypes have a greater bearing on the outcome of these interactions. Quantifying these interactions can provide valuable information on potential recruitment success among individuals and will further our understanding on overall population dynamics. It is more important than ever to gain this knowledge as most sturgeon species are under considerable threat, including Lake Sturgeon (Peterson et al. 2007), and hatchery production to support wild populations is a prevalent conservation tool (Schram et al. 1999; Jackson et al. 2002; Auer 2004). Superior growth rate is often used as a measure of success within aquaculture programs (Bryden et al. 2004), yet it has been reported among salmonid species that culture conditions may unwittingly select for maladapted individuals following release (Huntingford 2004). It is understood that maintaining high genetic diversity is important within these restoration attempts (Pikitch et al. 2005; Drauch and Rhodes 2007). If it is found that Lake Sturgeon populations consist of individuals with fixed feeding behaviours, maintaining phenotypic variability

within groups of stocked fish would be just as important.

The primary objective of this study was to determine if absolute size or underlying behavioural phenotypes better explain competitive asymmetries during foraging events among Lake Sturgeon cohort members. When the assumption of equal competitive ability among foraging individuals within an ideal free distribution (Fretwell and Lucas 1970) is replaced with the more realistic scenario of unequal competitors, it has been predicted that the more competitive individuals will be distributed within the most profitable feeding patch (Parker and Sutherland 1986). Using a two patch system (good and poor), it was predicted that if faster growth is the result of size-independent factors (e.g., behavioural phenotypes), then size-matched individuals previously determined to be fast-growers would spend a higher than expected proportion of time in the good feeding patch and monopolize these areas, spend a greater proportion of time engaged in feeding activity, and waste less time moving between patches than similarly sized cohort members previously determined to be slow-growers. Alternatively, if foraging interactions are driven more by size-dependent factors, it was predicted that larger juvenile Lake Sturgeon allowed to feed alongside smaller individuals would monopolize the profitable foraging patch, spend a greater amount of time feeding and spend less time moving between patches.

Methods

Experimental animals

Juvenile Lake Sturgeon used in this study were the progeny of wild Winnipeg River stock, hatched at the Canadian Rivers Institute Field Station, Pinawa, Manitoba during the spring of 2008 and reared in the Animal Holding Facility at the University of

Manitoba, Winnipeg, Manitoba. Prior to experimentation, individuals were maintained in tanks supplied with flow-through de-chlorinated tap water at a constant temperature of 15°C (± 1°C). Fish were exposed to a 12:12 h light:dark photoperiod.

Comparison between previously fast- and slow-growing juvenile Lake Sturgeon, controlled for absolute size (e.g., size-independent factors), was accomplished by first sorting larval fish following one month of exogenous feeding into two size classes, 'largest' and 'smallest', and then allowing the sturgeon to continue growing under these new living arrangements for an additional 5 month period. Over time, a number of initially slow-growing individuals caught up in size to those that were classified as fast-growing. At the point of experimentation the mean ± SD length and weight of 27 'slow-growing' individuals used in the study were 123.4 ± 8.3 mm and 6.5 ± 1.4 g, respectively. The mean ± SD length and weight of 27 'fast-growing' Lake Sturgeon were 120.8 ± 5.8 mm and 6.0 ± 0.9 g, respectively.

Comparison of feeding behaviours between juvenile Lake Sturgeon having different relative sizes (e.g., size-dependent factors), utilized individuals from stock tanks that had remained together since the start of exogenous feeding (i.e., did not undergo sorting). The mean ± SD length and weight of 27 'small' juvenile Lake Sturgeon used in the experiment were 107.6 ± 4.1 mm and 4.1 ± 0.4 g, respectively, while the mean ± SD length and weight of the 27 'large' fish were 169.0 ± 14.4 mm and 18.5 ± 4.7 g, respectively.

Experimental set-up

Three glass aquaria (74 cm L x 30 cm W x 40 cm H) were used simultaneously in this experiment. Environmental conditions outlined above were maintained throughout

the study with the exception that aquaria were equipped with a small charcoal filter and air stones to accommodate a recirculation water system. White bristol board covering the back and side walls of each aquarium, and desk lamps positioned directly above tanks, aided in the video recordings of each feeding event. Under the framework of an Ideal Free Distribution (Fretwell and Lucas 1970), experiments were conducted using a two-patch environment (good and poor). Feeders were fashioned after those used by Abrahams (1989) and consisted of modified 2-L Erlenmeyer flasks designed to distribute bloodworm (Diptera: Chironomidae; Hikari, Hayward, CA) through plastic feeding bars connected to the base of the flask. Food was released over a period of 15 min into the aquarium at a constant rate by sealing the flask with a rubber stopper, apart from a slow leak created by puncturing the stopper with a hypodermic needle. Placing feeders on magnetic stir plates kept the bloodworm from settling to the bottom of the flasks and ensured an even distribution of bloodworm to fish throughout feeding events. Food catchment trays positioned below feeders captured uneaten bloodworm in order to maintain a constant ratio of incoming resources between the two feeding patches (Figure 3.1).

Each feeding trial consisted of a group of six juvenile Lake Sturgeon free to interact with one another. For example, in assessing size-independent feeding behaviours among sturgeon, three individuals representing initially fast-growers and three individuals representing initially slow-growers were placed into the same experimental aquarium. The same arrangement was undertaken when assessing the feeding behaviours among sturgeon of different relative sizes. Experiments assessing size-independent and size-dependent feeding interactions were both replicated nine times.

The six individuals used per feeding trial were weighed prior to placement within the aquarium and bloodworm offered per feeding event was 10% of the total body mass (i.e., sum of the six fish). Care was taken to size match individuals within each replicate group comparing potential behavioural phenotypes, as well as within the 'large' and 'small' groups of fish when comparing feeding behaviours between sturgeon of different relative sizes. To distinguish individuals classified as 'fast-growing' and 'slow-growing', small pieces of different coloured acetate were attached to the dorsal musculature via clear thread. These individuals were anaesthetized using clove oil prior to the process and allowed one week to recover before being subjected to the experiment. Juvenile sturgeon used to compare feeding behaviour among 'large' and 'small' individuals were not externally marked in this study.

Feeding trials ran for three consecutive days and consisted of two feeding events daily between the hours of 09:00-10:30 and 18:30-20:00 hrs CST. Prior to each feeding event, filters and aerators were turned off and lamps were switched on. Day 1 was used to acclimate the sturgeon to their surroundings and learn to use the experimental feeders. During acclimation, food was distributed equally between both feeders. On days 2 and 3, bloodworm was divided 2:1 between feeders creating 'good' and 'poor' feeding patches. For each group tested, patch allocation between the left and right sides was decided randomly on day 2 and reversed on day 3. Feeding events were recorded using a Panasonic WV-CP484 camera (Panasonic, Osaka, Japan) with a Pentax 3.5-8 mm F/1.4 CS auto iris lens (Pentax, Tokyo, Japan) and observations at each 30 sec sample point (see below) were made from these continuous recordings. The need for high resolution to distinguish the external marks on the sturgeon of different growth backgrounds required

that the camera be positioned close to the tank. As a result, it was decided that the focus would remain on the good feeding patch during each feeding event. This criterion was not required during experimentation comparing sturgeon of different sizes and the camera was positioned in such a way to capture the behaviour within the good and poor feeding patches simultaneously.

Presence in good patch

The proportion of fast-growing/large and slow-growing/small sturgeon present in the good patch for each of the nine replicate groups tested was determined from counting the presence of individuals every 30 seconds over the course of each 15 min recorded feeding event. The mean of these 30 observations was calculated to determine the distribution of fish per feeding event, followed by taking the mean value of the four feeding events to represent the replicate group tested. The overall mean proportion of each subgroup tested (i.e., fast-growing, slow-growing, large and small) was determined from taking the average value of the nine replicates. A vertical line drawn down the center of the back of the aquarium aided in determining whether the tip of the sturgeon's snout crossed into the good feeding patch (Figure 3.1). Comparisons between the final mean proportion of fast- versus slow-growing and large versus small sturgeon present in the good patch were undertaken with two sample t-tests. For each group of sturgeon tested, the observed proportion of time spent in the good feeding patch was compared to the expected ideal free distribution (67%), as well as, a random distribution (50%) using one sample t-tests. Statistical computations, and all those described hereafter, were performed with the SYSTAT 9 statistical software package (SPSS Inc., 1998). Differences were considered statistically significant where $P \leq 0.05$.

Activity in good patch

At each 30 second sample point taken during the 15 min feeding trial, fish located within the good feeding patch were classified as participating in one of three behaviours, 1) Feeding - in contact with the food catchment tray, 2) Swimming - active but not in contact with the food catchment tray, or 3) Resting - not moving and not in contact with the food catchment tray. For each of the sturgeon subgroups tested (i.e., fast-growing, slow-growing, large and small), the mean number of individuals observed feeding, swimming and resting over the course of a 15 min feeding event (i.e., 30 observations) was divided by three to parse the data on a per individual basis. The overall mean proportion of juvenile Lake Sturgeon engaged in these activities was determined by first taking the mean value from the four feeding trials (per replicate) and then calculating the overall activity means from each of the nine replicated groups. To clarify, adding up the final mean activity values for each sturgeon subgroup would equal the total mean proportion of time spent in the good patch. Values were arcsin transformed prior to statistical analysis in order to satisfy the assumption of normality and equal variances. A one-way multivariate analysis of variance (MANOVA) was conducted to determine if subgroup (i.e., slow- vs. fast-growing or large vs. small) had an effect on activity choice.

Foraging activity between good and poor patches (size-dependent study)

Information on the estimated feeding activity (i.e., contact with the food catchment tray) among sturgeon of different relative sizes within both the good and poor patches was possible to quantify *a posteriori* due to the positioning of the camera during the study. This activity was evaluated in the same way as described above, with the difference being that information was gathered from the food catchment tray positioned

on the left side of aquaria (arbitrarily chosen). As such, mean values of feeding activity within the good and poor feeding patches were calculated from only two feeding events, respectively, and applied to each replicated group. This procedure satisfied the assumption of independent sampling when applying statistical computations. Final mean values were calculated using the nine replicate groups tested. Values were arcsin transformed prior to statistical analysis in order to satisfy the assumption of normality and equal variances. Two sample t-tests were conducted to compare the mean estimated feeding activity between the good and poor patches for the large and small sturgeon.

Monopolizing the good patch

The food catchment tray located beneath the feeder distributing over half of the total amount of bloodworm was assumed to be the most desired location to be stationed during a feeding event. With that assumption in mind, the willingness of fast and slow-growing, or large and small, individuals to feed together in this particular space was assessed by recording one of four possible feeding scenarios at every 30 sec observation taken during the 15 min feeding trial – 1) fast-growing/large sturgeon present and slow-growing/small sturgeon absent, 2) both fast-growing/large and slow-growing/small sturgeon present, 3) slow-growing/small sturgeon present and fast-growing/large sturgeon absent, and 4) both fast-growing/large and slow-growing/small sturgeon absent. An overall count of each feeding scenario per replicate group was completed by summing results across the four feeding trials. The overall count per subgroup was then calculated by summing results from each replicated group of fish. A Chi-square statistic was used to determine if the presence of slow-growing/small individuals was independent of the presence of fast-growing/large individuals.

Switching index between feeding patches

The number of individuals recorded as present in the profitable patch provided a means to estimate overall movement across the aquarium's centerline by noting additions and subtraction of bodies between each 30 sec observation. Crossings, irrespective of direction, were noted for each sturgeon subgroup tested (i.e., fast- and slow-growing, or large and small) during each 15 min feeding event. The final mean number of centerline crossings for sturgeon of different prior growth rates and current absolute sizes was determined by first taking the mean from each of the four feeding events per replicate and then calculating the mean of the nine replicate groups tested, respectively. Comparisons between the final mean number of patch switches for fast versus slow-growing and large versus small sturgeon were undertaken with two sample t-tests.

Results

Size-independent foraging study

The proportion of time spent within the good feeding patch was not significantly different between juvenile Lake Sturgeon of different prior growth rates but having similar absolute body sizes during experimentation (t = -1.029, df = 16, P = 0.310; Figure 3.2). The mean proportion of time spent by slow-growing fish within the good patch was slightly higher but not significantly so than their faster-growing tank mates (Figure 3.2). Lake Sturgeon spent significantly less time in the good patch than would be expected from the ideal free distribution (Table 3.1). In fact, the outcome was not significantly different from that which would be expected with random patch selection (e.g., 50% presence in the good patch; Table 3.1).

Prior growth rate (i.e., fast or slow) did not have a significant effect on activity

choice (i.e., feeding, swimming or resting) during feeding events (one-way MANOVA, $F_{3,14} = 0.392$, P = 0.760; Figure 3.3). Neither was the presence of previously slow-growers on the food-catchment tray in the good foraging patch associated with the presence of previously fast-growers (Yates' Chi-square test, $\chi^2 = 0.03$, P = 0.862). For instance, the overall count of the four feeding scenarios - 1) fast-growers present and slow-growers absent, 2) both fast- and slow-growers present, 3) slow-growers present and fast-growers absent and 4) neither group present - was 190, 550, 255 and 85, respectively.

The estimated number of times individuals crossed the aquarium centerline was not significantly different between juvenile Lake Sturgeon of different growth rate backgrounds (t = 1.515, df = 16, P = 0.149; Figure 3.4).

Size-dependent foraging study

In conducting experiments between large and small individuals, three of the nine replicate groups contained at least one study fish that remained inactive throughout the course of the four feeding events. These individuals did not participate in any feeding interactions and remained motionless during the 15 min feeding event. It is unclear if these juveniles represent the same or different individuals throughout the experiment, as they were not externally marked. Interestingly, it was only juvenile sturgeon of the relatively large size classification that displayed this behaviour. As such, analysis of the feeding interactions between large and small foraging individuals include data sets with all nine replicates and data sets with only the six replicates containing full participation of study fish.

The proportion of time spent within the good feeding patch was not significantly different between juvenile Lake Sturgeon of different absolute sizes, whether including

all nine replicates (t = -1.537, df = 16, P = 0.144; Figure 3.2) or only the six replicates where there was full participation by study fish during feeding events (t = -0.184, df = 10, P = 0.858; Figure 3.2). As was observed in the size-independent study, all Lake Sturgeon spent significantly less time in the good patch than would be expected from the ideal free distribution (Table 3.1, Figure 3.2). However, only the large individuals spent time in each patch that was not significantly different from random selection (e.g. 50% presence in good patch; Table 3.1, Figure 3.2). The relatively smaller individuals were found to occur in the good patch significantly more often than would be expected from random selection, regardless of participation levels among study fish during feeding events (Table 3.1, Figure 3.2).

Relative size (i.e., large or small) had no significant effect on the activity choice of juvenile Lake Sturgeon when incorporating data from all nine replicates (one-way MANOVA, $F_{3,14} = 1.490$, P = 0.260; Figure 3.3) or the six replicates with full participation (one-way MANOVA, $F_{3,8} = 1.272$, P = 0.348; Figure 3.3). Overall, large and small Lake Sturgeon were found to engage in foraging activity 1.6 times more often in the good patch than in the poor patch when incorporating all replicates, and this was a significant difference (Table 3.2). This outcome is much more representative of an ideal free distribution, although discrepancies emerged when dividing the data by fish subgroup. For instance, it was the smaller individuals that drove this result as they spent just over twice the amount of time foraging in the good patch than the poor patch while larger individuals spent nearly equal time between the two patches (Table 3.2). Excluding the replicates which contained less than full participation by study fish during feeding events led to no overall differences in foraging activity between feeding patches.

However, mean foraging activity was always higher in the good patch (Table 3.2).

The presence of small juvenile Lake Sturgeon on the food catchment tray located in the good patch was found to be significantly dependent on the presence of large fish when all replicate groups were included in analysis (Yates' Chi-square test, n = 9, χ^2 = 7.47, P = 0.006). Overall counts for each feeding scenario – 1) large present, small absent, 2) large and small present, 3) small present, large absent, and 4) neither group present – were 266, 313, 313 and 188, respectively. However, when only the six replicates with full foraging participation were included in analysis, the presence of small fish on the food catchment tray was not significantly dependent on the presence of large individuals (Yates' Chi-square test, n = 6, χ^2 = 0.24, P = 0.624). Overall counts for each feeding scenario (see above) were 254, 247, 113 and 106, respectively.

As in the size-independent study, the estimated number of times large and small individuals crossed the aquarium centerline was not significantly different from each other whether there was full participation during feeding events (n = 6, t = 0.268, df = 10, P = 0.794; Figure 3.4) or not (n = 9, t = 0.950, df = 16, P = 0.356; Figure 3.4).

Discussion

Under the framework of an unequal competitors ideal free distribution (Parker and Sutherland 1986) it was hypothesized that if fast-growing and (or) large juvenile Lake Sturgeon were competitively superior to their slower-growing and smaller tank mates, the fast-growers and (or) large fish would spend a greater than expected proportion of time in the good foraging patch. This was not the case. Vandersteen Tymchuk et al. (2005) found that growth-hormone-transgenic Coho Salmon, *Oncorhynchus kisutch*, were also not more successful at acquiring food in the profitable patch than size-matched non-

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transgenic individuals, even though they were expected to be better competitors. However, low statistical power was cited as a possible reason for this outcome. Milinski (1984) reported that competitively superior Three-spined sticklebacks, *Gasterosteus aculeatus*, were not overrepresented in the good feeding patch when feeding alongside inferior competitors. Rather, he determined that the most competitive individuals were the first to distribute themselves according to patch profitability, followed by the least competitive individuals, resulting in no apparent deviations from the expected ideal free distribution. Had the juvenile Lake Sturgeon subgroups (i.e., fast- and slow-growing; large and small) tested in this study adhered to an ideal free distribution, this may have been a plausible explanation for the outcome of this experiment. As it were, the spatial distributions of the subgroups tested seemed to more closely resemble random patch choice. Underrepresentation within profitable foraging patches is a common occurrence and can indicate departures from the assumptions of an ideal free distribution (Kennedy and Gray 1993). Barth (2011) also noted this in studies on wild juvenile Lake Sturgeon where adherence to an ideal free distribution was not observed in relation to food availability along a stretch of the Winnipeg River, Manitoba.

The perception limit model (Abrahams 1986) and interference model (Sutherland 1983) are two attempts to quantify violations of the 'ideal knowledge' and 'free movement' assumptions that are at the core of the ideal free distribution. As the output is similar for each violation, it can be difficult to distinguish the mechanism at play in empirical datasets. Abrahams (1986) suggested that the specific violation could be determined *a posteriori*, if data were available on the net individual intake rates. The author further explains that this is because the perception limit model predicts net intake

rates by individuals in the good foraging patch to be greater than for those individuals in the poor foraging patch. Unfortunately, individual ingestion rates were not recorded in this study as it was not possible to differentiate between successful and unsuccessful capture rates given the bottom-feeding behaviour of the study species. Additionally, the focus of this study was exclusively on the activity within the good foraging patch. That said, the central position of the camera during comparisons among sturgeon of different relative sizes made it possible to compare the feeding activity occurring within the good and poor foraging patches, *a posteriori*. This revealed that, contrary to an overall tank distribution nearing 1:1, the distribution of feeding individuals throughout all replicates (n = 9) was 1.6 to 1, a much closer fit to the expected 2 to 1 distribution of an ideal free distribution (Fretwell and Lucas 1970). Therefore, it may be that the study fish were capable of differentiating between the good and poor foraging patches but were not always in a position to access the food (i.e., violations of the 'free movement' assumption). However, there were no significant differences detected between the proportion of individuals feeding in the good and poor foraging patches when assessing large individuals independent of small individuals or when assessing replicates with full participation (n = 6). Therefore, it seems more plausible that individuals were unable to differentiate poor from good foraging patches (i.e., violations of the 'ideal knowledge' assumption). The experimental set-up may have factored into the above results. For instance, Lake Sturgeon feeding behaviour is dependent on olfactory cues (Kasumyan 2002), and the relatively short distance between the two feeding patches (10 cm) may have been insufficient for individuals to detect the different resource levels.

It was also hypothesized that if fast-growing and (or) large juvenile Lake

Sturgeon were competitively superior to their slower-growing and smaller tank mates, the fast-growers and (or) large fish would spend a greater proportion of time feeding in the good foraging patch and monopolize the food catchment tray. However, there was no evidence in the current study to support this. There was also no evidence to suggest that fish phenotype had any bearing on activity choice during foraging events within either the size-independent or size-dependent foraging studies. The latter result was somewhat unexpected because negative interactions between relatively large and small individuals have been reported in other sturgeon species. Sbikin and Budayev (1991) observed smaller Stellate Sturgeon, *A. stellatus,* individuals being pushed into the water column by larger conspecifics and termed this behaviour 'pseudo-hierarchic' as the authors did not feel the behaviour was deliberate. Kynard and Horgan (2002) observed larger Shortnose Sturgeon, *A. brevirostrum*, and Atlantic Sturgeon, *A. oxyrinchus oxyrinchus*, charging, pushing and biting smaller conspecifics immediately upon placing fish within experimental tanks. However, the authors noted that the more aggressive behaviours subsided after a day or two. Finally, Allen et al. (2009) did not observe any aggressive behaviours among large Lake Sturgeon towards smaller tank mates following a one week acclimation period.

Passive and aggressive interactions such as those reported by Sbikin and Budayev (1991) and Kynard and Horgan (2002), respectively, were not quantified in the present study. However, even if such behaviours existed among the sturgeon in this study, they likely had little bearing on the ability of smaller individuals to access resources. There was no evidence to suggest that large or fast-growing individuals monopolized the food catchment tray. That said, the specific location of individuals on the food catchment tray

was not documented and may have potentially played a role in the ability of individuals to access food. Juvenile Atlantic Salmon occupying marginal locations within either the good or poor foraging patches experienced lower food intake rates than those positioned centrally (MacLean et al. 2005) and subordinate juvenile common cranes, *Grus grus*, fed along the periphery of good foraging patches when in the presence of more dominant adults (Bautista et al. 1995). Additional study quantifying ingestion rates by Lake Sturgeon individuals during group foraging events is needed.

Patch switching was quantified in this study as it has potential bearing on both the ability of individuals to differentiate between patch quality (Milinski 1984; Milinski 1994; Koops and Abrahams 2003), as well as, provide an indication of any negative interactions among individuals (Maclean et al. 2005). Milinski (1984) observed variable patch switching among groups of size-matched sticklebacks and determined that the poor competitors switched patches more often than good competitors. Godin and Keenleyside (1984) went so far as to term fish 'stayers' and 'switchers' when similar observations were made among cichlid fish. However, there was no indication in the present study to suggest that relatively small or previously slow-growing juvenile Lake Sturgeon switched patches more often than their larger or previously faster-growing tank mates. The stimulus behind observed patch switching in the current study is unknown but may simply be spontaneous movement. Even among groups of juvenile Atlantic Salmon, *Salmo salar*, that consisted of individuals displaying aggressive behaviours, 56% of patch switches were deemed to be the result of spontaneous activity (Maclean et al. 2005). Furthermore, sturgeon are known to react to olfactory stimuli by moving in an oscillatory motion (Kasumyan 1999), a behaviour that would likely increase the occurrence of

centerline crossings.

Previous study assessing Lake Sturgeon growth rate variability indicated that group interactions among larval fish during feeding events influenced size divergence over time (see Chapter 2). However, the present study looking at group interactions among juvenile Lake Sturgeon during feeding interactions could not determine what factors may have contributed most to unequal food acquisition. Juvenile Lake Sturgeon representing different subgroups based on size-independent factors (size matched previously fast- and slow-growers) and size-dependent factors (different relative sizes) did not adhere to an unequal competitors ideal free distribution as outlined by Parker and Sutherland (1986). No interacting subgroup monopolized optimal foraging areas within the experimental set-up or showed significantly different rates of patch-switching. As such, it is not possible to suggest that any one subgroup was a better competitor than another following the current study. Study fish did not adhere to an ideal free distribution as described by Fretwell and Lucas (1970) and it may be that the fish were unable to differentiate between the resource levels in each patch, as presented. Adjustments to the study design should be undertaken in future assessments.

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Table 3.1. Results of one sample t-tests between the observed and predicted presence of Lake Sturgeon groups in the good foraging patch (i.e., ideal free distribution or random). Bolded values indicate significant differences at P ≤ 0.05.

| Sturgeon Subgroup | Observed Presence in Good Patch | | df | Predicted Presence in Good Patch | | | |
| | | | | 0.67 | | 0.50 | |
	mean	± SE		t-value	P =	t-value	P =
Fast (n = 9)	0.512	0.020	8	-7.98	**0.000**	0.62	0.550
Slow (n =9)	0.545	0.025	8	-5.00	**0.001**	1.81	0.109
Large (n = 9)	0.494	0.043	8	-4.06	**0.004**	-0.13	0.899
Small (n = 9)	0.573	0.028	8	-3.45	**0.009**	2.63	**0.030**
Large (n = 6)	0.552	0.036	5	-3.30	**0.021**	1.45	0.206
Small (n = 6)	0.559	0.018	5	-6.20	**0.002**	3.33	**0.021**

Table 3.2. Results of paired sample t-tests between the proportion of large and small juvenile Lake Sturgeon feeding within the good and poor foraging patches. Values were arcsin transformed prior to statistical analysis. Bolded values indicate significant differences at $P \leq 0.05$.

Sturgeon Subgroup	Foraging in Good Patch		Foraging in Poor Patch		df	t-value	P=
	mean	± SE	mean	± SE			
All (n = 9)	0.274	0.034	0.170	0.027	8	3.040	**0.016**
Large (n = 9)	0.229	0.049	0.196	0.037	8	0.751	0.474
Small (n = 9)	0.318	0.062	0.145	0.034	8	2.673	**0.028**
All (n = 6)	0.280	0.038	0.214	0.023	5	2.083	0.092
Large (n = 6)	0.290	0.046	0.251	0.029	5	0.570	0.593
Small (n = 6)	0.269	0.079	0.177	0.043	5	1.968	0.106
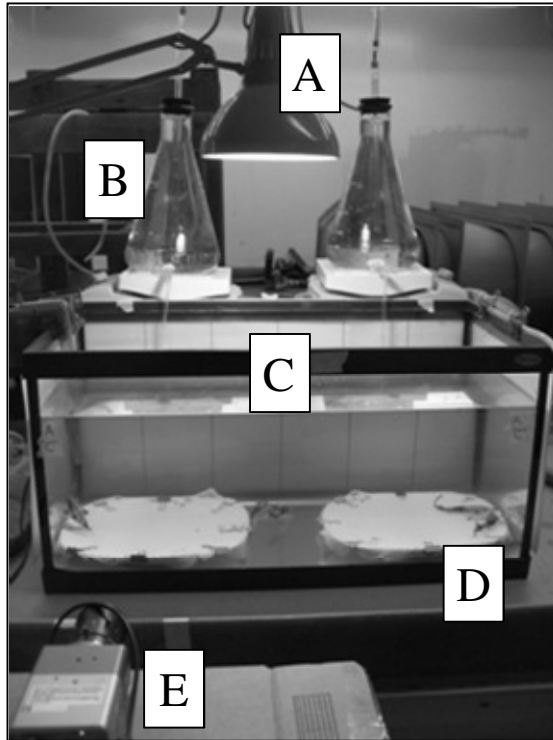
Figure 3.1. Experimental set-up to compare foraging behaviour of juvenile Lake Sturgeon including (A) lamp, (B) feeders, (C) aquarium, (D) food catchment trays and (E) video camera.
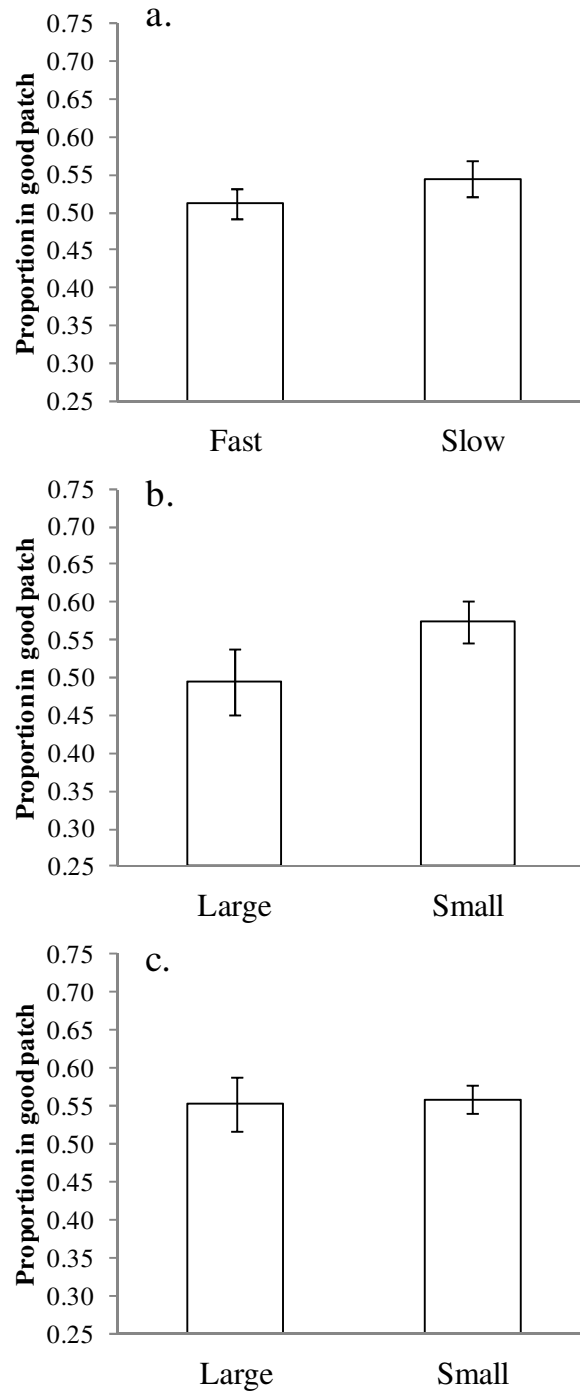
Figure 3.2. Mean proportion (±SE) of Lake Sturgeon in the good feeding patch (67% of the available food) that had a) different prior growth rates but size-matched (n=9), b) different absolute sizes but less than full participation of study fish during feeding events (n=9) and c) different absolute sizes with full participation of study fish (n = 6).
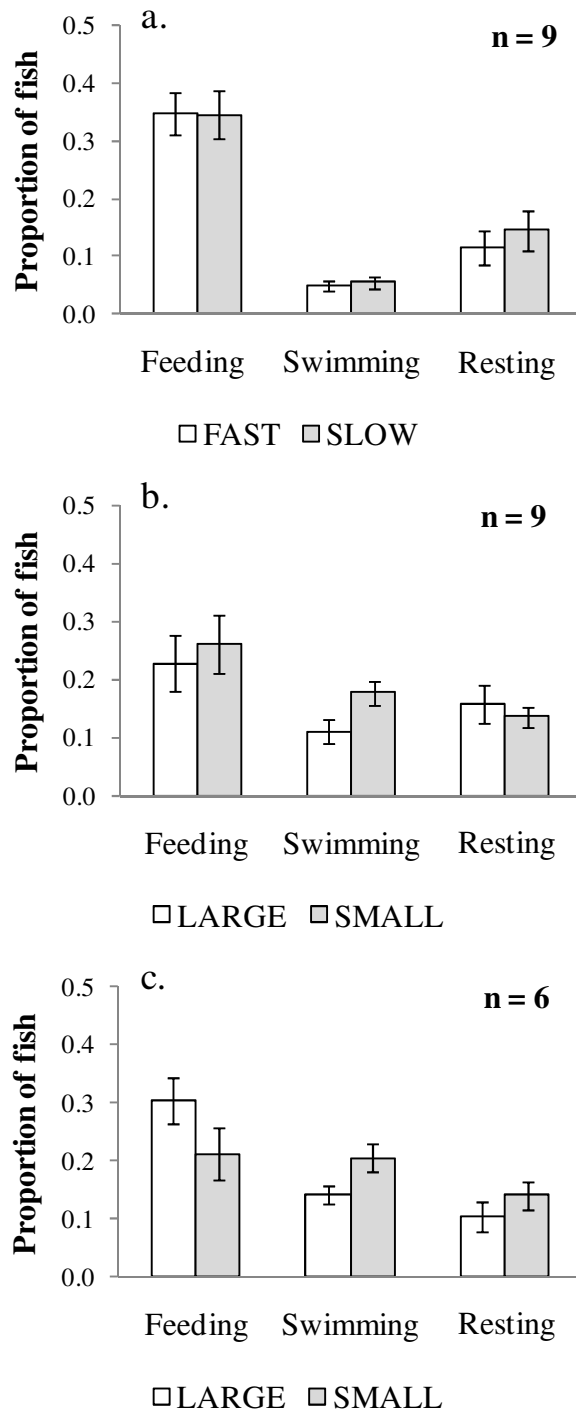
Figure 3.3. Mean proportion (± SE) of Lake Sturgeon feeding, swimming and resting in the good feeding patch (i.e., 67% of the available food) that had (a) different prior growth rates but size-matched (n=9), b) different relative sizes but less than full participation of study fish during feeding events (n=9) and c) different relative sizes with full participation of study fish (n = 6).
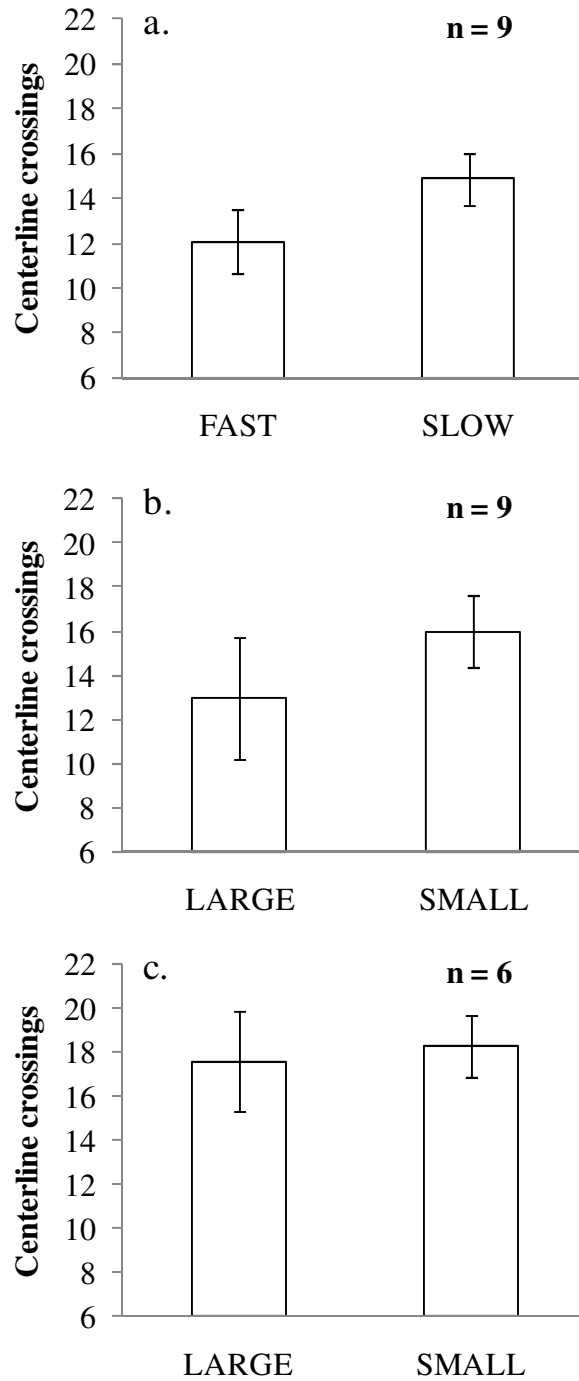
Figure 3.4. Mean estimated number of centerline crossings (±SE) among juvenile Lake Sturgeon that had a) different prior growth rates but size-matched (n=9), b) different absolute sizes but less than full participation (n=9) and c) different absolute sizes with full participation (n = 6).

Chapter 4

Effect of body size on the performance of juvenile Lake Sturgeon during a
low water temperature challenge

Abstract

The 'critical size and period' hypothesis predicts that faster growing individuals within a cohort are expected to have a greater probability of surviving their first winter, particularly when the growing season is short. Lake Sturgeon, *Acipenser fulvescens*, occupies some of the most northerly distributions of any sturgeon species and populations experience extended periods when resources may be limited. To assess the influence of size on juvenile Lake Sturgeon subjected to a low water temperature challenge, survival, body condition, plasma glucose and triglyceride levels were compared between relatively large and small individuals at various points throughout the study. Sampling points corresponded to a temperature reduction from 16.5 °C to 4 °C over three weeks, four weeks at 4 °C, 8 weeks at 4 °C and a temperature increase from 4 °C back to 16.5 °C over a three week period. Although it was predicted that the larger juveniles would outperform smaller conspecifics in this study, there was no difference in survival, body condition or plasma glucose and triglyceride levels between large and small individuals. Feed was offered throughout the study and it is thought that this allowed the smaller individuals to perform on par with larger members of the same cohort. Swimming activity during feeding events was also assessed among study groups and, although activity decreased significantly following the temperature reduction, groups continued to feed over the two-month period at the coldest temperature. Results suggest that both large and small juvenile Lake Sturgeon are capable of acclimating to a low water temperature of 4 °C and are able to utilize food resources, if available, such that survival and body condition remain high.

Introduction

A number of factors can be expected to influence year-class strength among fish species including, but not limited to, the number of participating spawners, environmental conditions during egg incubation, summer growing conditions and winter severity (Hurst and Conover 1998; Shaw et al. 2012). Among north-temperate fish populations, considerable study has focused on overwinter survival and, furthermore, on the effect that size has on the ability of individuals to endure periods of low water temperature and reduced feeding opportunities. Beamish and Mahnken (2001) proposed the 'critical size and period hypothesis', which states that larger individuals have a greater chance of surviving to spring than smaller conspecifics. Size-selective overwintering mortality within fish populations is a much researched topic and, for the most part, results have confirmed the notion that bigger is better (Biro et al. 2004; Pangle et al. 2004; Sutton and Ney 2001; Hurst and Conover 1998; Henderson et al. 1988). These outcomes are primarily attributed to the fact that smaller individuals exhaust energy reserves faster than larger individuals due to the combined effect of having a reduced capacity for initial energy storage and higher mass-specific metabolic rates (Xiaojun and Ruyung 1990; Cargnelli and Gross 1997; Biro et al. 2004). Starvation is just one of several mechanisms that can cause winter mortality, mechanisms that include thermal stress, predation, and pathogens, all of which tend to select against the smallest members of a cohort (reviewed in Hurst 2007). However, some studies have reported an advantage for the smaller individuals of a cohort under unusually warm winter conditions and reduced food availability (Schultz and Conover 1999; Connolly and Petersen 2003), as smaller individuals require lower resource levels than larger individuals to sustain themselves

(Werner 1994). At higher latitudes where more severe winter conditions are expected, mortality may be less dependent on size (Garvey et al. 1998). Despite the seemingly disproportionate attention that body size receives in overwintering studies, it is more likely that survival depends on a number of interactions including temperature, food, predation and geography (Connolly and Petersen 2003; Hurst 2007).

Ectotherms have a number of physiological and behavioural options for coping with low water temperatures and (or) starvation. Fish often enter into a torpor-like state, also termed dormancy, whereby activity rates, metabolic rates, and subsequent energy expenditure are dramatically reduced (Lemons and Crawshaw 1985; McCue 2010). When feeding activity ceases, individuals mobilize endogenous reserves. This includes the mobilization of liver glycogen, lipids and (or) proteins, most often utilized in this order but also known to be species specific (Navarro and Gutierrez 1995; Gillis and Ballantyne 1996; Hsieh and Shiau 2000; Pérez-Jiménez et al. 2007; Furné et al. 2008).

Sturgeon species are restricted to the temperate waters of the Northern Hemisphere (Billard and Lecointre 2001; Auer 2004) and Lake Sturgeon, *Acipenser fulvescens*, together with Siberian Sturgeon, *A. baerii*, inhabits the most northerly distribution and coldest waters of all sturgeon species (Artyuklin 1995). Lake Sturgeon numbers are currently below historic levels and most populations are listed as rare or threatened (Peterson et al. 2003). Increasing population numbers will depend on the recruitment of strong year-classes, which has been shown to be influenced by the ability of young-of-the-year (YOY) to survive their first winter (Post and Evans 1989; Hurst and Conover 1998). As such, it is imperative that conservation biologists focus their attention on the overwinter survival of Lake Sturgeon, particularly during the first few years of life

when juveniles are expected to be at their most vulnerable. Furthermore, conservation of this species has resulted in proactive management strategies including the stocking of hatchery-cultured fish, which, due to economic and spatial constraints, are generally released in the autumn of their first year (Brown and Day 2002; Pikitch et al. 2005). Size variability is prevalent among hatchery-reared Lake Sturgeon cohorts (see Chapter 2), and the influence this may have on subsequent stocking success is unknown. To date, research has focused on the performance of sturgeon in response to low temperatures (Kappenman et al. 2009) and following periods of starvation (Gillis and Ballantyne 1996); however, research looking at how these two factors influence sturgeon of different sizes is lacking.

The primary objective of this study was to compare the performance of relatively large and small Lake Sturgeon from the same cohort over the course of a low temperature challenge as measured by survival, body condition, plasma glucose and triglyceride levels. It was hypothesized that all study variables would decrease in juvenile Lake Sturgeon subjected to an extended period of low water temperatures but that the smallest individuals would be more affected than the largest individuals. Group activity rates were also assessed to provide additional insight into the ability of juvenile Lake Sturgeon to feed when subjected to low water temperatures. It was hypothesized that activity rates would be dramatically reduced at low water temperatures.

Methods

Experimental animals

Juvenile Lake Sturgeon used in this study were the progeny of wild Winnipeg River stock, hatched at the Canadian Rivers Institute Field Station, Pinawa, Manitoba

during the spring of 2009 and reared in the Animal Holding Facility at the University of Manitoba, Winnipeg, Manitoba. Prior to experimentation, individuals were maintained in tanks supplied with flow-through de-chlorinated tap water at a temperature of 15 °C ± 1 °C. Fish were fed frozen bloodworm (Hikari, Hayward, CA) daily and exposed to a 12:12 hr light:dark photoperiod.

This study utilized 50 large (mean ±SD, total length 237.7 ± 16.2 mm, weight 39.6 ± 8.1 g) and 50 small (mean ±SD, total length 171.3 ± 15.8 mm, weight 15.1 ± 3.8 g) one-year-old Lake Sturgeon from three family groups of the same cohort that had remained separated since hatch. Each family group was represented in both the large and small size-classes and across experimental tanks, and thus was not figured into later analysis. All fish were individually marked with numbered Monel fin tags (National Band and Tag Company, Newport, KY) along the leading edge of the pectoral fin prior to being placed in experimental tanks.

Experimental conditions

Five oval shaped tanks (45 gallon capacity) were set-up within a temperature-controlled room in the Animal Holding Facility, University of Manitoba and covered with semi-transparent plastic at all times except feeding events. Flow-through de-chlorinated tap water was delivered to tanks via three lines providing hot (27 °C), moderate (16 °C) and cold (2 °C) water, accommodating a large range of water temperatures through flow rate adjustments.

Ten large and ten small Lake Sturgeon were distributed within each of five experimental tanks and allowed to interact freely. Figure 4.1 summarizes the daily mean tank temperature and feeding schedule for experimental animals within this study. A

temperature of 16.5 °C was held constant for three weeks prior to reducing the temperatures. During the acclimation period, experimental animals were offered chopped squid at 10% body mass (BM) daily. The amount of squid offered to groups of fish within each tank was determined following initial body measurements and adjusted following each subsequent measurement event throughout the study. A drop in water temperature to the targeted 4 °C was completed within a three-week period by lowering temperatures daily (mean ±SD, 0.58 ±0.68 °C). Feeding rates were also reduced with decreasing water temperatures. Chopped squid was offered at rates of 8% body mass (BM) daily between 12 °C and16 °C, 5% BM daily between 4 °C and 12 °C, and 1% BM at 4 °C. Between weeks 6 and 14 fish were fed every other day with some exceptions. The extent to which wild juvenile Lake Sturgeon of the same population feed during winter months is unknown, and so the arbitrarily selected feeding rates may either be an under or, more likely, over representation of natural conditions. Individuals were maintained at 4 °C for two months at which point water temperatures were increased to 16.5 °C (daily mean ±SD, 0.60 ±0.86 °C). Feeding rate adjustments were completed as outlined above.

The study occurred over a 17-week period between 29 November, 2010 and 28 March, 2011 and performance of Lake Sturgeon for each variable assessed (see below) occurred at five points throughout the study including Week 3 – after acclimation to 16.5 °C, Week 6 – after the temperature drop from 16.5 to 4 °C, Week 10 – after one month at 4 °C, Week 14 – after two months at 4 °C, and Week 17 – after the temperature increase from 4 °C to 16.5 °C. As it was necessary to sacrifice a subsample of individuals in each tank and because this subsequently affected overall tank densities which would be

expected to influence several of the variables assessed (e.g., length, body mass and activity), one tank was randomly selected at each check point after which time the remaining fish within these tanks were eliminated from further study. To clarify, the fish within Tank 2, 4, 3, 5 and 1 were sampled at Weeks 3, 6, 10, 14 and 17, respectively.

Survival and body condition

Experimental tanks were checked daily and deceased fish were removed upon first observation. The number of large and small individuals remaining in the five experimental tanks following each study week were plotted to observe mortality trends. Final survival comparisons between large and small Lake Sturgeon were conducted for each tank using a two-tailed Fisher's Exact Test due to small sample sizes.

Fork length (± 1 mm), total length (± 1 mm) and body mass (± 0.1 g) measurements were taken at Week 0, 3, 6, 10, 14 and 17 of the study. Juvenile Lake Sturgeon from all tanks not yet sacrificed were included in measuring, and feeding rates were adjusted in relation to the total body mass within the tank. One exception was the Week 3 sampling period when only the Lake Sturgeon within the tank of interest were measured (e.g., Tank 2). Condition factor, K_{FL}, was calculated using the following equation (after Fulton 1911 *in* Ricker 1975):

$$K = M \ x \ 10^5 \div FL^3,$$

where M = body mass (g) and FL = fork length (mm).

Fork length (FL), total length (TL), body mass (BM), and Condition factor (K_{FL}) were compared between large and small fish (across tanks) and among tanks (irrespective of fish size) at the start of the study (i.e., Week 0) using a two-way analysis of variance (ANOVA). Similar analyses were undertaken at each subsequent sampling week (i.e.,

Week 3, 6, 10, 14, 17) using the values obtained from fish held within the tank randomly selected for assessment on that date. Where significant differences were detected between means, analysis was followed with the Newman-Keuls multiple comparison test.

Plasma sampling and assays

Lake Sturgeon were euthanized by immersion in an overdose of tricaine methanesulphonate (MS-222; 250 parts per million (ppm)) and then immediately bled from the caudal sinus. Blood samples were collected in heparinized tubes and immediately centrifuged using an Accuspin Micro 17R (Fisher Scientific, Pittsburgh, PA) at 10,000 rpm for 4 minutes at 4 °C. Plasma was removed using disposable Pasteur pipettes, transferred to 1.5 ml free-standing tubes and stored at -80°C until analysis. Blood samples were collected from individuals approximately 24 hours following the last feeding event, as this has been suggested to be the optimal point for assessing baseline biochemical parameters (Shi et al. 2010). Sampling occurred over several hours; therefore, blood was collected from alternating large and small individuals to account for potential differences in plasma glucose and plasma triglyceride levels at various times of the day.

Commercial assay kits (Wako Chemicals USA, Inc., Richmond, VA) were used to determine glucose (LabAssay[TM] Glucose) and triglyceride (LabAssay[TM] Triglyceride) concentrations in the plasma samples. The glucose assay was based on an enzymatic method with a combination of mutarotase and glucose oxidase. The triglyceride assay was based on an enzymatic method using N-ethyl-N-(2-hydroxy-3-sulfopropyl)-3,5-dimethoxyaniline sodium salt (DAOS) as a blue pigment. Standards, along with samples, were placed in transparent 96-well microplates in triplicate prior to being placed in a

microplate reader.

Plasma glucose (mg/dL) and triglyceride (mg/dL) levels were determined for 5 large and 5 small individuals from a randomly selected tank at each sampling week. For each variable, comparisons were made between the two fish sizes (across sampling weeks) and among sampling weeks (regardless of fish size) using a two-way ANOVA. Where significant differences were detected among means, analysis was followed with the Newman-Keuls multiple comparison test.

Activity rates

Prior to each of the five sampling events, activity levels were quantified for juvenile Lake Sturgeon from all remaining experimental tanks (e.g., n = 5 at Week 3, n = 4 at Week 6, etc.). This was accomplished by positioning five digital video cameras (Panasonic, Osaka, Japan) with 5-50 mm lenses (Pentax, Tokyo, Japan) above each tank and recording activity for a one-hour period following the removal of tank covers. Activity rates were quantified at a later date by counting the number of fish that passed the tank's center line (width-wise) within a 15 second window at three foraging stages: 1) half an hour prior to feeding, 2) during feeding, and 3) half an hour after food introduction. The activity rates of large and small individuals were not quantified separately due to the difficulty of distinguishing the size of fish during highly active periods.

Activity rates were compared among the three foraging stages (regardless of study week) and across sampling weeks (irrespective of foraging stage) using a two-way ANOVA. Where significant differences were detected among means, analysis was followed with the Newman-Keuls multiple comparison test. Statistical analyses were

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completed using NCSS (Hintze 2004) at a significance level of $P \leq 0.05$.

Results

Survival and body condition

Overall survival rates were high within this study for both large (80 to 90%) and small (60 to 100%) juvenile Lake Sturgeon, as well as across tanks (70 to 95%). No significant differences were detected between the survival of large and small individuals within any of the experimental tanks (Figure 4.2). Interestingly, the majority of mortalities occurred during the acclimation period (i.e., first 3 weeks of study) and no mortalities occurred following Week 4 (Figure 4.2).

At the start of the low water temperature challenge, there were no significant interactions between the two size groups and five tanks when assessing FL ($F_{4,90} = 0.43$, $P = 0.79$), TL ($F_{4,90} = 0.21$, $P = 0.93$), BM ($F_{4,90} = 0.38$, $P = 0.83$) and K_{FL} ($F_{4,90} = 0.31$, $P = 0.87$) among juvenile Lake Sturgeon using a two-way ANOVA. Therefore, comparisons were made between the size groups and tanks independently of each other. Analysis confirmed that individuals classified as large had significantly larger FL ($F_{1,90} = 407.7$, $P < 0.001$; Figure 4.3), TL ($F_{1,90} = 409.7$, $P < 0.001$; Figure 4.4), BM ($F_{1,90} = 363.1$, $P < 0.001$; Figure 4.5) and K_{FL} ($F_{1,90} = 4.4$, $P = 0.04$; Figure 4.6) than conspecifics classified as small. It was also found that there were no significant differences in FL ($F_{4,90} = 0.57$, $P = 0.69$; Figure 4.3), TL ($F_{4,90} = 0.59$, $P = 0.67$; Figure 4.4), BM ($F_{4,90} = 0.69$, $P = 0.60$; Figure 4.5) and K_{FL} ($F_{4,90} = 0.70$, $P = 0.60$; Figure 4.6) among fish in each of the five tanks, a result that was important due to the lack of tank replication in subsequent sampling events.

During the 17-week study there were no significant interactions between the two

size groups and five sampling periods (i.e., tanks) when assessing FL ($F_{4,72}$ = 0.38, P = 0.82), TL ($F_{4,72}$ = 0.23, P = 0.92), BM ($F_{4,72}$ = 0.12, P = 0.97) and K_{FL} ($F_{4,72}$ = 0.71, P = 0.56) among juvenile Lake Sturgeon using a two-way ANOVA. Therefore, comparisons were made between size groups and sampling periods independently of each other. Juvenile Lake Sturgeon initially classified as large remained significantly larger in FL ($F_{1,72}$ = 325.2, P < 0.001; Figure 4.3), TL ($F_{1,72}$ = 334.4, P < 0.001; Figure 4.4) and BM ($F_{1,72}$ = 253.3, P < 0.001; Figure 4.5) than their initially smaller conspecifics. However, despite the fact that relatively larger Lake Sturgeon had greater body condition at the start of the study, there was no significant difference in K_{FL} between the two size groups throughout the experimental period ($F_{1,72}$ = 0.26, P = 0.61; Figure 4.6).

Significant differences were not detected among sampling periods (i.e., tanks) for FL ($F_{4,72}$ = 0.38, P = 0.68; Figure 4.3), TL ($F_{4,72}$ = 0.70, P = 0.59; Figure 4.4) and BM ($F_{4,72}$ = 1.14, P = 0.35; Figure 4.5). However, significant differences were detected among sampling periods for K_{FL} ($F_{4,72}$ = 2.87, P = 0.03; Figure 4.6) and condition of fish at Week-6 and Week-17 were found to be higher than at Week-3.

Plasma glucose & triglyceride levels

Mean glucose and triglyceride levels were assessed following the three-week acclimation period and at designated sampling events thereafter. No significant interactions were detected between the two sizes of Lake Sturgeon subjected to the low water temperature challenge and the sampling week (i.e., tanks) for plasma glucose ($F_{4,40}$ = 0.18, P = 0.95) or triglyceride ($F_{4,40}$ = 0.34, P = 0.85) levels using a two-way ANOVA. As such, comparisons between the two sizes and five sampling periods (i.e., tanks) with respect to glucose and triglyceride values were conducted independently of each other.

No significant differences were detected for plasma glucose ($F_{1,40}$ = 2.05, P = 0.16; Figure 4.7) or triglyceride ($F_{1,40}$ = 0.67, P = 0.42; Figure 4.8) levels between large and small juvenile Lake Sturgeon. In contrast, significant differences in plasma glucose levels were detected among sampling periods ($F_{4,40}$ = 3.28, P = 0.02; Figure 4.7) and it was further determined that levels at week-6 (i.e., tank 4) were significantly higher than at either week-3 (i.e., tank 2) or week-10 (i.e., tank 3). Triglyceride levels were not found to be significantly different among sampling events throughout the study ($F_{4,40}$ = 1.9, P = 0.13; Figure 4.8).

Activity rates

The mean number of times juvenile Lake Sturgeon crossed the tank centerline was assessed at three phases during feeding events, in addition to, the five sampling points within this study. No significant interaction was detected between the feeding phases and sampling points ($F_{8,30}$ = 0.86, P = 0.56). Therefore, activity rate was assessed for the two factors independently. The greatest number of centerline crossings occurred prior to feeding events and this result was statistically significant ($F_{2,30}$ = 7.5, P < 0.01; Figure 4.9). However, of primary interest was the number of centerline crossings in relation to water temperature and it was found that a significantly higher number of crossings occurred when water temperatures were at 16.5 °C than at 4 °C ($F_{4,30}$ = 26.04, P < 0.001; Figure 4.9). It is also of some interest that, although not significant, the number of centerline crossings by fish did increase incrementally over time when held at 4 °C.

Discussion

The primary objective of this research was to assess the performance of large and small juvenile Lake Sturgeon of the same cohort when challenged with reduced water

temperatures and feedings. As expected, behavioural and physiological attributes tested

did change with decreasing temperature but not always in the predicted fashion and with

little to no discernable difference among individuals of different relative sizes. The

temperature challenge used in the present study was likely an underestimate of the harsh

conditions that this species would experience within their most northerly range and, as

such, there is reason to believe that the parameters of this experiment did not present as

great a challenge to the study fish as was initially sought. For instance, wild Lake

Sturgeon within a stretch of the Winnipeg River tagged with acoustic transmitters capable

of recording temperature were found to occupy waters < 4 °C during the months of

December to March (McDougall 2011). Nevertheless, the results warrant review and may

be pertinent to individuals located in more southerly ranges.

Survival under winter-like conditions is most often related to large fish size

(Henderson et al. 1988; Pangle et al. 2004); however, survival was high throughout each

phase of the current study for both size-classes tested. The results observed in this study

are likely a product of providing feeding opportunities throughout the experiment. Other

studies that assessed fish performance under low water temperatures, and incorporated

both a fed and starved treatment, generally reported significantly greater survival rates

among the fed groups (Thompson et al. 1991; Hurst and Conover 2001; Biro et al. 2004;

Pangle et al. 2004). McCollum et al. (2003), however, related high mortalities among

age-0 White Crappies, *Pomoxis annularis*, to the duration of winter-like conditions (173

days vs. 6 days at < 4 °C) and not to the feeding regime (fed or starved) or to fish size.

Therefore, an alternative hypothesis for the high survival experienced by both size-

classes in this study could be that the temperature challenge was simply too 'mild' to

trigger significant mortality events. Diet source (i.e., chopped squid) may have also played a significant role in survival rates of study animals, as Rennert et al. (2005) attributed survival rates among Zander, *Sander lucioperca*, not to fish size, but rather to the fat content and its fatty acid composition in the feed prior to experiencing winter conditions.

Interestingly, the greatest number of mortalities among both size-classes occurred during the acclimation period and primarily within a two-week period following transfer to the experimental tanks. Sorting and transportation procedures between stock and experimental tanks were relatively brief (< 1 hour); however, it may be that the combined effect of tank transfer, handling associated with initial measurements and the tagging procedure produced enough of a stressor to generate mortality among some fish. A few individuals died during the first week of temperature reduction; however, no mortalities occurred in the study following week-4.

Body condition (K_{FL}) was used in the present study as an indicator of fish health and, although it was hypothesized that smaller individuals would have lower body condition than larger conspecifics following the study, such an outcome was not observed. This was unexpected but presumed to be another result greatly influenced by the level of feed offered during the low water temperature challenge. For example, relatively smaller juvenile Bluegills, *Lepomis macrochirus*, were found to consume 1.0 to 2.5% BM daily in comparison to only 0.4 to 0.8% BM daily among larger conspecifics during a low water temperature challenge (Shoup and Wahl 2011). Disproportionate acquisition of feed among the two size-classes may have also occurred in the present study leading to greater body condition among smaller individuals. In fact, 1% BM

offered daily was enough to support continued growth among young-of-the-year Great

Sturgeon, *Huso huso*, at water temperatures of 10 °C (Falahatkar et al. 2013). These

results are in contrast to those found in juvenile Shovelnose Sturgeon where reduced

weights and exhausted energy reserves occurred at temperatures below 12 °C, despite

being fed throughout the study (Kappenman et al. 2009).

Morphometric indices are not always reliable predictors of energy content

(Congleton and Wagner 2006; McCue 2010). As such, plasma glucose and triglyceride

levels were compared among Lake Sturgeon subjected to low water temperatures and

reduced feeding levels as blood-borne metabolites are known to reflect the net production

and utilization by the tissues in fish (Gillis and Ballantyne 1996). Overall, mean plasma

glucose levels among Lake Sturgeon in the current study ranged between 65 and 100

mg/dL and these values are comparable to similarly-aged Lake Sturgeon from other

studies (55 to 80 mg/dL, Gillis and Ballantyne 1996; 60 to 90 mg/dL, Allen et al. 2009).

Unexpectedly, smaller juveniles did not have significantly lower plasma glucose levels

than larger individuals in this study. In addition, plasma glucose levels remained

relatively constant throughout the study with the exception of rising levels during

sampling weeks 6 and 17. Sub-yearling White Sturgeon, *A. transmontanus*, starved over

10 weeks had significantly lower plasma glucose levels at the end of the study than at the

start (Hung et al. 1997) suggesting that the Lake Sturgeon in the current study were likely

not compromised from a nutritional standpoint. However, Gillis and Ballantyne (1996)

reported that Lake Sturgeon starved over an 8-week period did not show significantly

different levels of plasma glucose concentrations in comparison to fed conspecifics, with

the exception of one sampling point 10 days following the start of the study. Indeed,

Costas et al. (2011) has suggested that, due to the importance of glucose as a fuel for a number of tissues, animals often have the ability to maintain glucose levels, even when starved, through a number of mechanisms including: reducing the rate of glucose utilization, increasing gluconeogenic and glycogenolitic potentials and (or) enhancing liver glucose exporting capacity. As such, plasma glucose in and of itself may be a poor indicator of fish health during a temperature and (or) feed challenge.

One possible explanation for the rising plasma glucose levels at the Week 6 and 17 sampling points is that the fish experienced thermal stress following temperature change events, despite a gradual and conservative temperature adjustment (< 1 °C daily). Circulating concentrations of glucose become elevated during stressful events as a result of released catecholamines which initiates glycogenolysis, a process that converts glycogen to glucose (Mazeaud et al. 1977) and plasma glucose levels are generally reported in studies examining stress in sturgeon (Cataldi et al. 1998; Barton et al. 2000; Allen et al. 2009; Falahatkar et al. 2009). For example, resting plasma glucose levels of Green Sturgeon, *A. medirostris*, rose significantly over a 21-day period when fish were subjected to daily acute stress events including chasing, water depth reductions or confinement (Lankford et al. 2005). As such, it is hypothesized that temperature adjustments in this study may have also been experienced as a daily acute stress event by the study fish. Furthermore, plasma glucose levels were highest following the temperature reduction phase (Week 6) and the low temperatures experienced by fish at this time may have played a role. Lankford et al. (2003) reported that Green Sturgeon subjected to an acute stress event at 11 °C had a rapid and prolonged increase in plasma glucose levels through 6 hours in comparison to a similar group subjected to the same

stressor at 19 °C. The authors suggested that the elevated glucose levels detected in the plasma at the colder temperature was due to reduced glucose uptake by the tissues. Following four weeks at a constant temperature of 4 °C, the Lake Sturgeon in the current study were found to have plasma glucose levels similar to those observed prior to the temperature reduction phase and future studies should assess this rate of recovery. From a practical perspective, these results may indicate a particularly sensitive period for juvenile Lake Sturgeon during the seasonal temperature changes, regardless of body size. Interestingly, higher mortalities have been reported among Brook Trout, *Salvelinus fontinalis*, in early winter months and are suggested to be the result of the physiological demands of cold temperature acclimation (Cunjak et al. 1987).

This study did not find a significant difference in triglyceride level among Lake Sturgeon of different sizes or over the duration of the 17-week experiment. Review of starvation studies indicates that plasma triglyceride may increase, as has been observed in starved Amur Sturgeon, *A. schrencki*, (Shi et al. 2010) and tilapia, *Oreochromis niloticus* x *O. aureus* (Hsieh and Shiau 2000). However, plasma triglyceride levels have also been reported to either decline over time such as in starved sub-yearling White Sturgeon (Hung et al. 1997) and European Seabass, *Dicentrarchus labrax*, (Pérez-Jiménez et al. 2007), or occur at levels lower than fed conspecifics such as in Common Carp, *Cyprinus carpio*, (Shemeno et al. 1997), Gilthead Sea Bream, *Sparus aurata*, (Polakof et al. 2006) Pacu, *Piaractus mesopotamicus*, (Takahashi et al. 2011) and Senegalese Sole, *Solea senegalensis*, (Costas et al. 2011). Reflecting these inconsistent patterns, Congleton and Wagner (2006) reported high variability of plasma triglyceride values among starved and fed juvenile salmonids, concluding that it was not a particularly useful index of

nutritional condition. The authors went on to report that plasma alkaline phosphatase (ALP) activities and total protein concentrations may be better blood-chemistry indicators of nutritional status than either plasma triglyceride or plasma glucose.

It was observed that fish in this study adopted a primarily sedentary existence at water temperatures below 11 °C. Negative correlations between water temperature and activity have been reported for juvenile Lake Sturgeon (Peake 1999), White Sturgeon (Crocker and Cech 1997) and Green Sturgeon (Mayfield and Cech 2004). Interestingly, it was observed that study fish were relatively quick to engage in food searching behaviour when a feeding event was merely anticipated (e.g., following removal of tank covers). As such, the significantly lower mean number of centerline crossings at the coldest temperature is suggested to be the result of reduced swimming speed of individuals and not a reduction in the overall number of active study fish. For instance, juvenile White Sturgeon had a mean swimming speed of approximately 675 cm s^{-1} at 16°C but only 50 cm s^{-1} when maintained at 10 °C (Crocker and Cech 1997). Likewise, young-of-the-year Striped Bass, *Morone saxatilis*, dropped to swimming speeds of 2.7 body lengths s^{-1} from 5 body lengths s^{-1} when maintained in water temperatures of 2 °C versus 8 °C, respectively (Hurst and Conover 2001).

The behaviour of Lake Sturgeon following removal of tank covers indicates that study fish were well trained to feeding events and, this unnatural conditioning, makes it difficult to make inferences about the feeding behaviour of wild juveniles during overwintering conditions. However, what is clear from this study is that juvenile Lake Sturgeon have the capacity to engage in foraging activity and utilize food resources at temperatures of 4 °C, if the opportunity presents itself. An intriguing observation in this

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study was that the juvenile Lake Sturgeon progressively increased their swimming activity rates over the two months maintained at a water temperature of 4 °C. This was an unexpected result and several hypotheses can be considered. First, it may be that energy reserves were depleted to a point that individuals were motivated to increase their food searching behaviour. For instance, there has been evidence of compensatory feeding responses among Striped Bass during both laboratory and field-based overwintering studies (Hurst and Conover 2003). Second, the observed increase in activity rate may be the result of acclimation to the reduced water temperatures such that swimming speeds increased with time. Few studies have looked at repeat swimming performance among fish prior to and following an acclimation period, particularly with respect to volitional swimming activity (O'Steen and Bennett 2003) and warrants further review. Finally, the consistent and predictable manner in which the food resources were offered to study animals during the water temperature challenge may have overridden an initial (and likely innate) response to reduce activity in order to conserve energy. Repeating the study under similar conditions, but with sporadic feedings (e.g., both in time and rates), would provide an opportunity to assess the potential tradeoffs of conserving energy or engaging in food searching behaviour, and the subsequent decisions made by study fish. Given that the Lake Sturgeon were consistently fed throughout the low water temperature challenge, it is most likely that either of the last two hypotheses, or a combination of those, would best explain the gradual increase in activity rates.

In conclusion, the results of this study indicate that smaller individuals within a Lake Sturgeon cohort are neither disadvantaged or advantaged relative to larger individuals of the same cohort under the environmental challenge presented in this study,

as defined by survival, body condition, and two plasma metabolites (i.e., glucose and triglyceride). However, the study did provide some unexpected results for the group as a whole, which may provide a starting point for future study on Lake Sturgeon biology and behaviour during overwintering conditions. For instance, there is reason to believe that the fish in this study found temperature reductions and increases to be a relatively stressful event. The juvenile Lake Sturgeon also appeared to adapt readily to a cold water environment, slightly increasing activity rates and maintaining high body conditions over a two month period at 4 °C. These results, if replicated under more refined experimentation, suggest that natural and artificial recruitment may be more dependent upon the cohort's ability to endure environmental fluctuations experienced in the autumn and spring and less on the severity and duration of the winter season. Further study is needed to assess overwintering survival among juvenile Lake Sturgeon and should incorporate laboratory experiments defining winter severity thresholds, and their effect on both large and small individuals of the same cohort.

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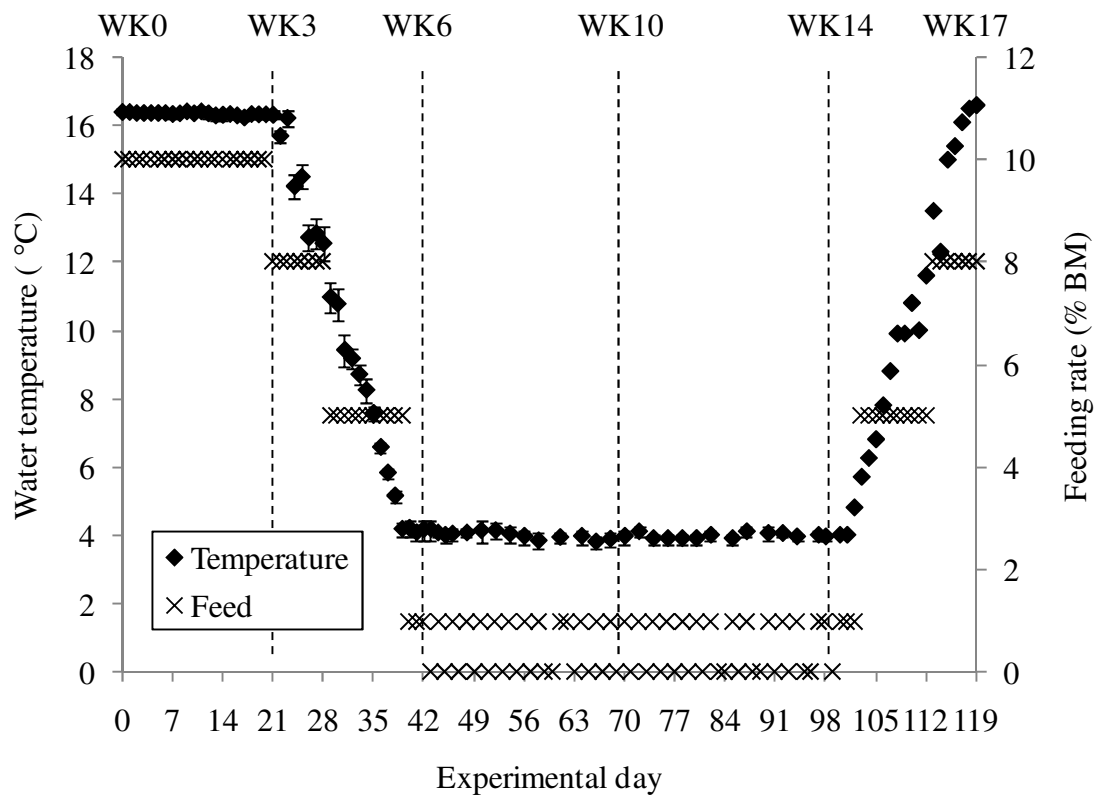
Figure 4.1 Mean (±SD) daily temperature among experimental tanks (n = 5 to 1) and daily feeding rate (% body mass) experienced by juvenile Lake Sturgeon in the present study. Broken lines indicate the weeks when fish measurements and blood plasma samples were taken.
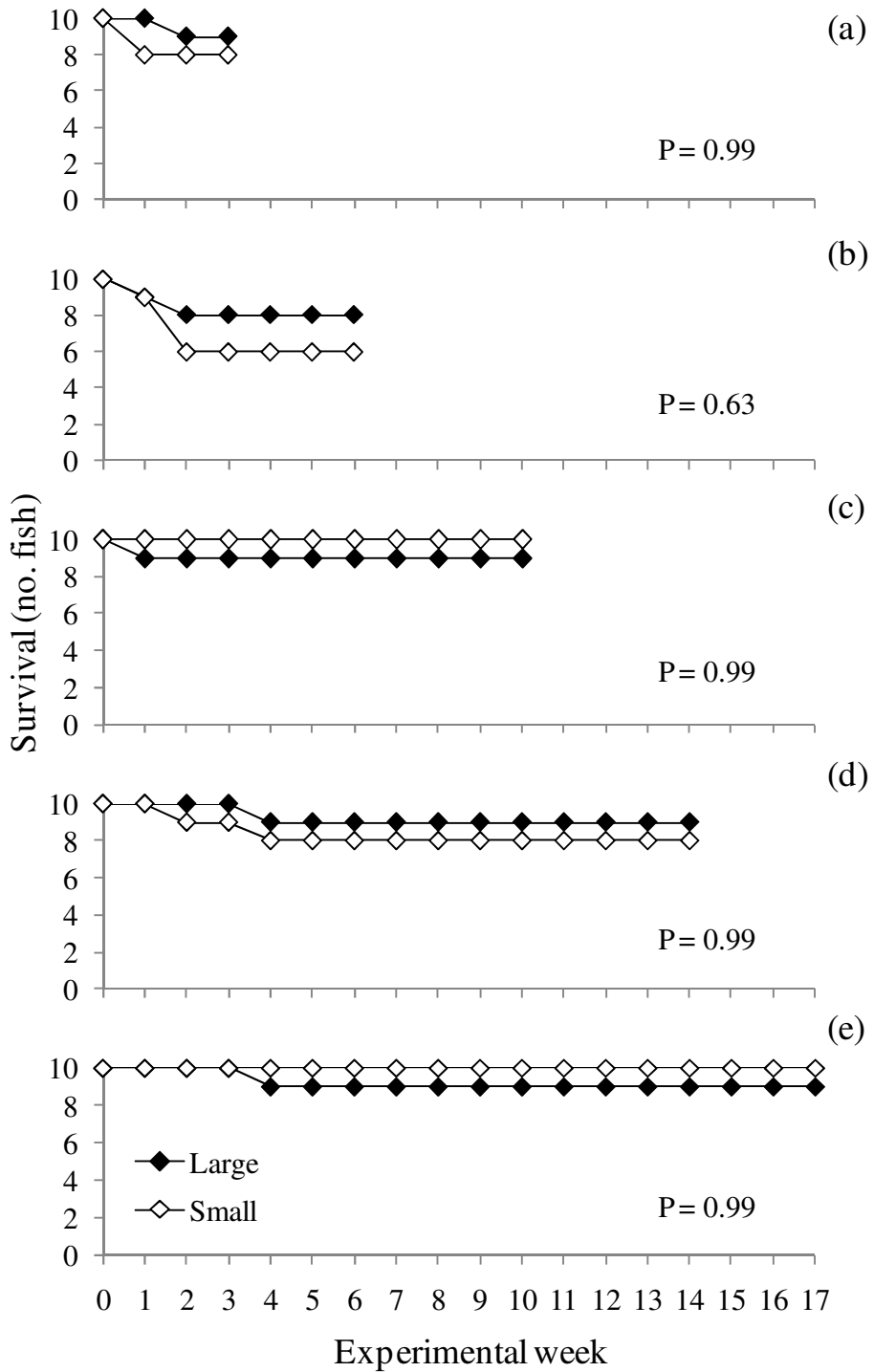
Figure 4.2 Weekly survival of large (n = 10) and small (n = 10) juvenile Lake Sturgeon in (a) Tank 2, (b) Tank 4, (c) Tank 3, (d) Tank 5 and (e) Tank 1. Final survival was compared between large and small individuals within each tank at the termination of study using a Fisher Exact Test at $P \leq 0.05$.
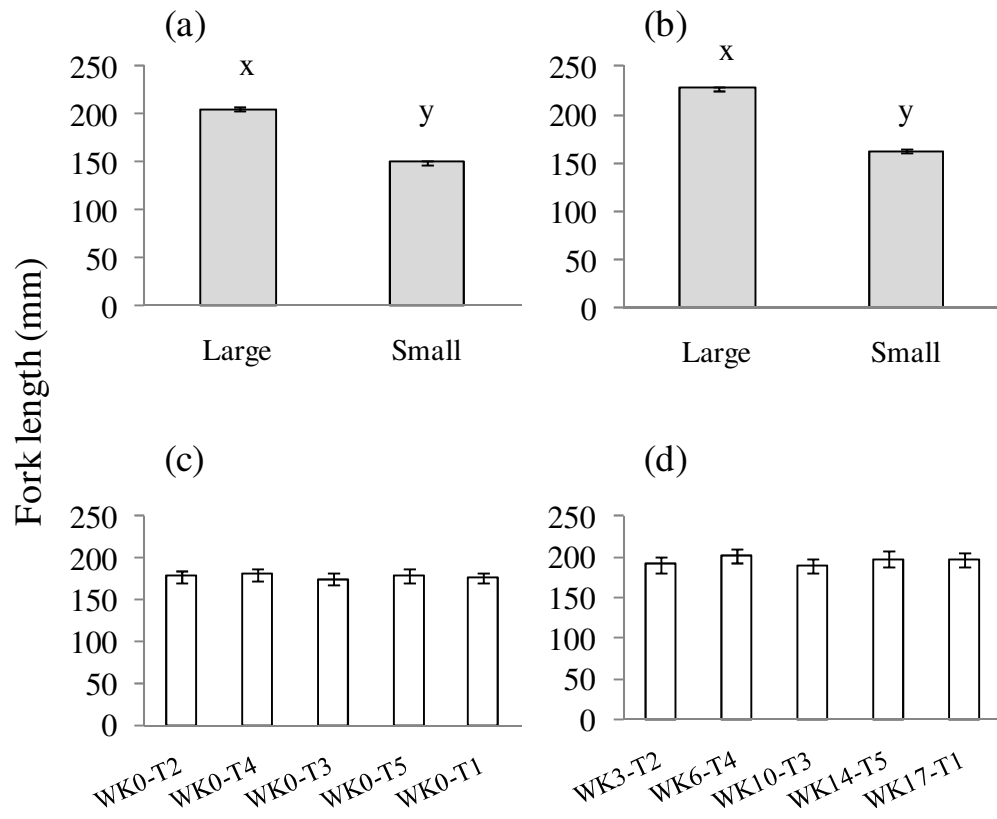
Figure 4.3 Mean fork length (±SE) of juvenile Lake Sturgeon at Week 0 (a,c) and at five sampling points during the study (b,d). Interactions were analysed with a two-way ANOVA and comparisons were conducted between two size groups (regardless of tank/study period) (a,b) and among tanks/study period (regardless of size groups) (c,d) where appropriate. Different letters indicate significant differences at $P \le 0.05$.
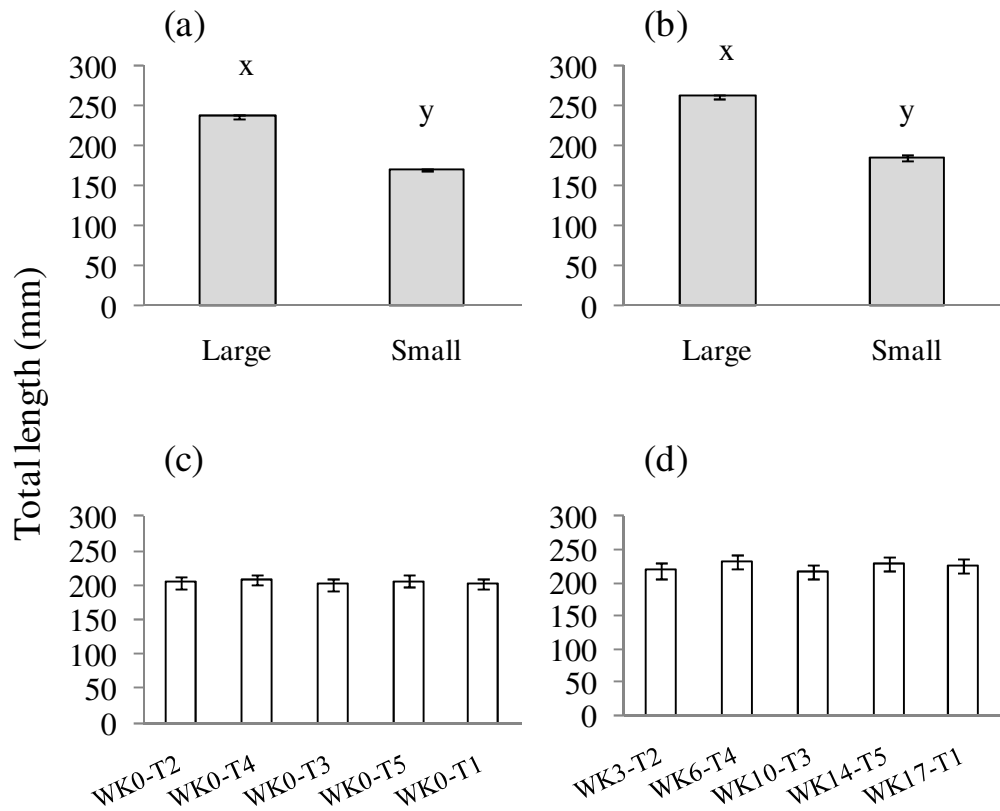
Figure 4.4 Mean total length (±SE) of juvenile Lake Sturgeon at Week 0
(a,c) and at five sampling points during the study (b,d). Interactions were
analysed with a two-way ANOVA and comparisons were conducted
between two size groups (regardless of tank/study period) (a,b) and
among tanks/study period (regardless of size groups) (c,d) where
appropriate. Different letters indicate significant differences at $P \leq 0.05$.
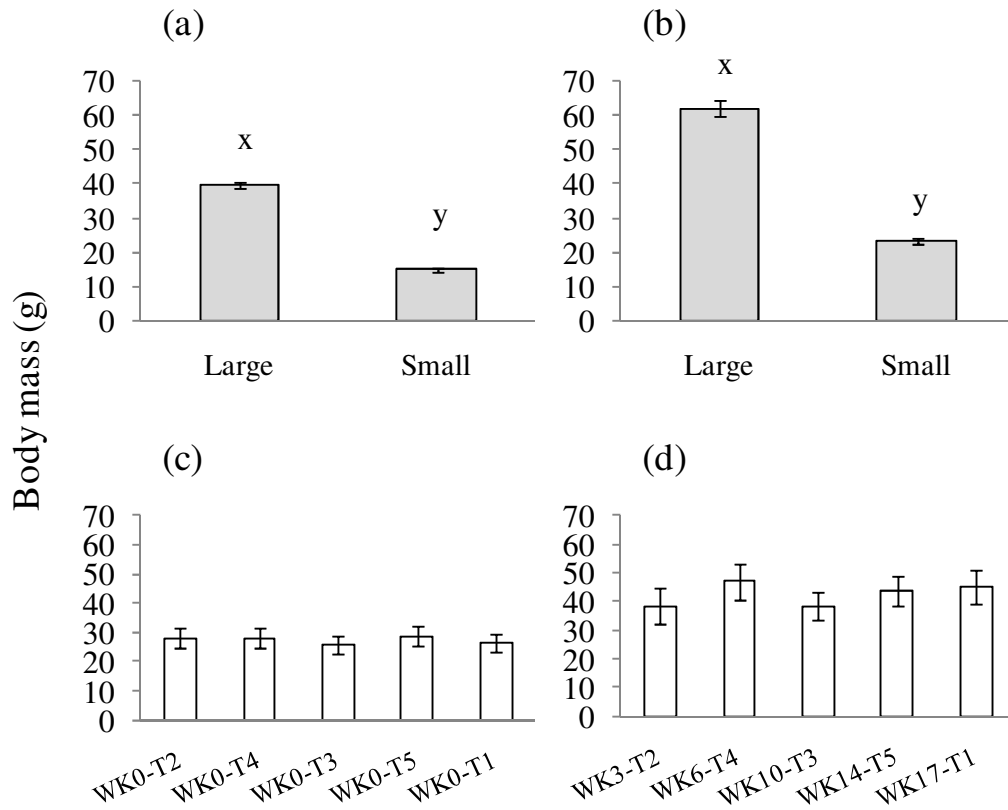
Figure 4.5 Mean body mass (±SE) of juvenile Lake Sturgeon at Week 0 (a,c) and at five sampling points during the study (b,d). Interactions were analysed with a two-way ANOVA and comparisons were conducted between two size groups (regardless of tank/study period) (a,b) and among tanks/study period (regardless of size groups) (c,d) where appropriate. Different letters indicate significant differences at $P \leq 0.05$.
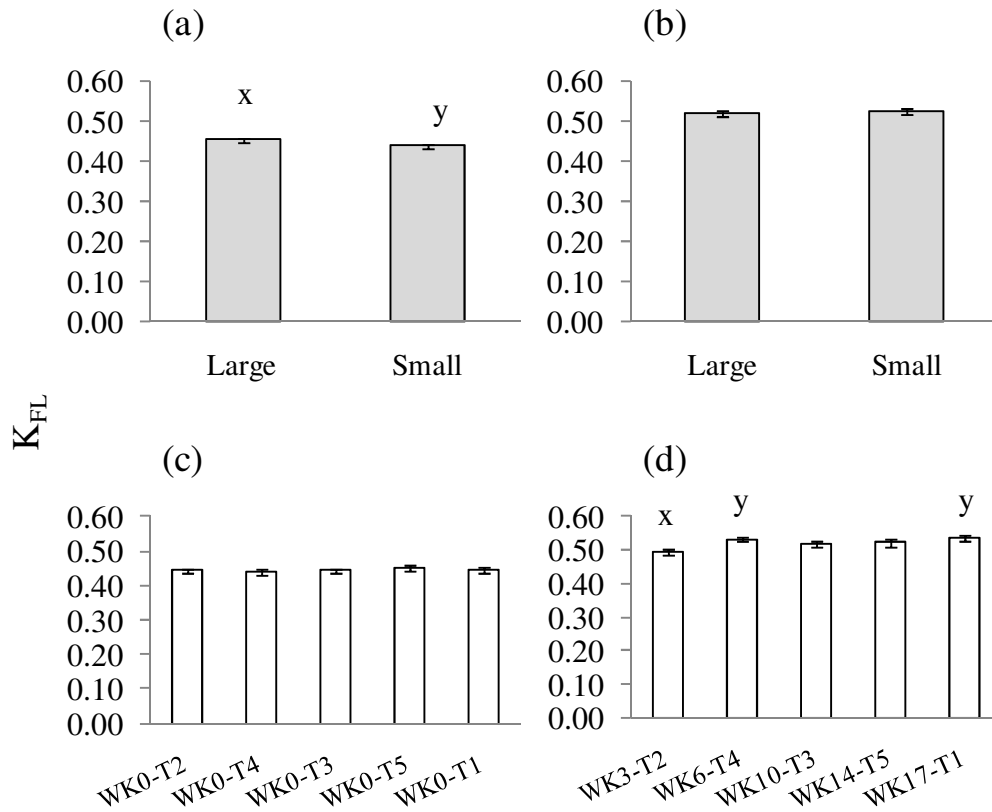
Figure 4.6 Mean condition (K_{FL}) (±SE) of juvenile Lake Sturgeon at Week 0 (a,c) and at five sampling points during the study (b,d). Interactions were analysed with a two-way ANOVA and comparisons were conducted between two size groups (regardless of tank/study period) (a,b) and among tanks/study period (regardless of size groups) (c,d) where appropriate. Different letters indicate significant differences at $P \le 0.05$.
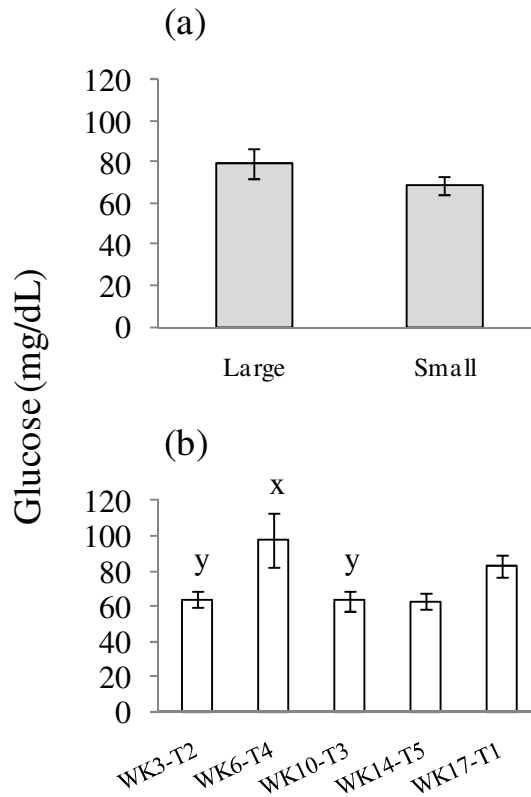
Figure 4.7 Mean plasma glucose levels (±SE) of juvenile Lake Sturgeon at five sampling points during the study. Interactions were analysed with a two-way ANOVA and comparisons were conducted between the two size groups (regardless of tank/study period) (a) and among tanks/study period (regardless of size groups) (b) where appropriate. Different letters indicate significant differences at $P \leq 0.05$.
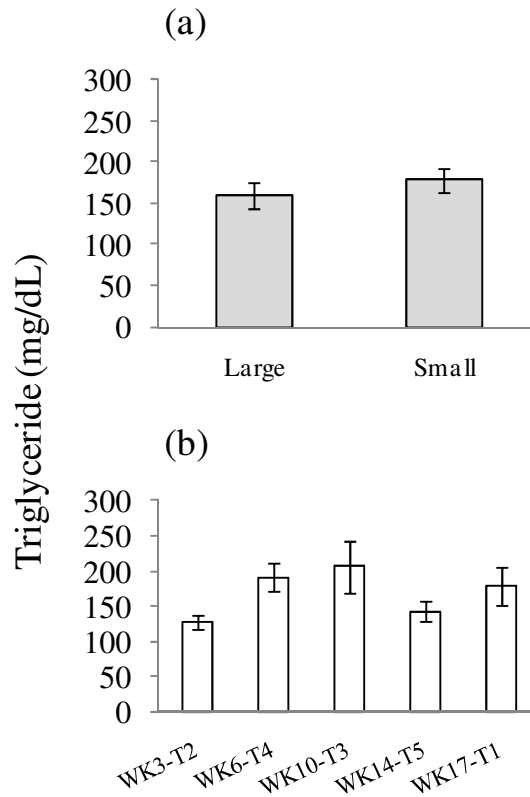
Figure 4.8 Mean plasma triglyceride levels (±SE) of juvenile Lake Sturgeon at five sampling points during the study. Interactions were analysed with a two-way ANOVA and comparisons were conducted between the two size groups (regardless of tank/study period) (a) and among tanks/study period (regardless of size groups) (b) where appropriate. Different letters indicate significant differences at $P \leq 0.05$.
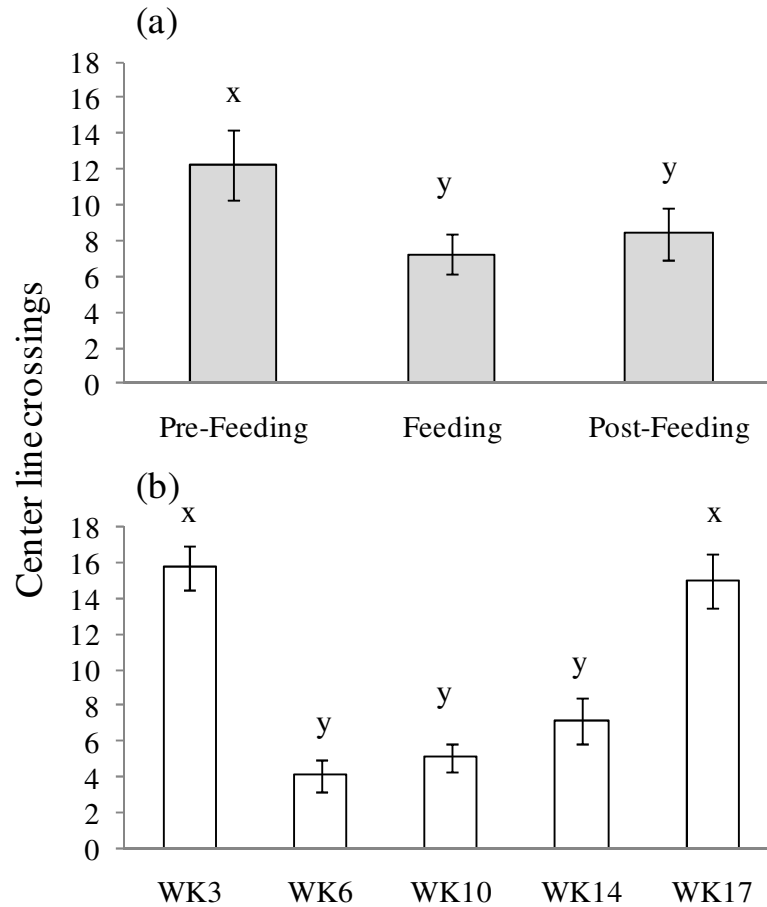
Figure 4.9 Mean number of centreline crossings (±SE) among juvenile Lake Sturgeon at five sampling points during the study. Interactions were analysed with a two-way ANOVA and comparisons were conducted for the three foraging stages (regardless of study period) (a) and for study periods (regardless of foraging stage) (b) where appropriate. Different letters indicate significant differences at $P \leq 0.05$.

Chapter 5

Relative recapture rate, movement and growth of age-0 and age-1 hatchery-reared Lake Sturgeon released into the Winnipeg River, Manitoba

Abstract

Artificially propagated Lake Sturgeon, *Acipenser fulvescens*, were released into the Winnipeg River, Manitoba as age-0 fall fingerlings (FF) or age-1 spring yearlings (SY) to determine the influence of age/size-at-release on relative recapture rate, movement and growth. A total of 10,000 FF (114.4 ± 6.1 mm Total Length, 5.4 ± 0.8 g) and 415 SY (244.0 ± 16.0 mm Total Length, 59.1 ± 11.7 g) were released, of which 51 individuals were recaptured and identified as hatchery-reared fish from previously applied fin clips and/or passive integrated transponder (PIT) tags over a two-year period. Gillnetting efforts from 2009 and 2010 showed that relative recapture rate was 24-fold greater for SY than FF. Lake Sturgeon released as yearlings also displayed higher site fidelity (100%) than FF (71%) and the mean total length $\pm$SD of SY (338.9 ± 23.3 g) recaptured at age-2 were significantly greater than similarly-aged FF (301.4 ± 55.0 mm). However, release location affected post-stocking performance among FF. For instance, FF were captured in greater numbers and displayed higher site fidelity following release into Numao Lake, a known nursery area for wild juveniles. One FF individual showed exceptional growth when located in a stretch of river known to have low Lake Sturgeon densities. Overall, the condition (K_{TL}) of hatchery-reared individuals was similar between SY (0.36 to 0.41) and FF (0.35 to 0.41), and comparable to wild juveniles of similar total lengths. Although length-at-release associated with different ages appears to influence post-release performance, inter-individual differences in size among hatchery-reared fish within stocking events could not be related to recaptures or movement distance.

Introduction

Lake Sturgeon, *Acipenser fulvescens*, are large cartilaginous fish inhabiting the fresh waters of the Great Lakes, Hudson-James Bay and Mississippi River watersheds (Scott and Crossman 1973). At the turn of the 20th Century, commercial exploitation led to a precipitous decline in Lake Sturgeon populations across North America (Harkness and Dymond 1961). Today, most Lake Sturgeon populations are protected and closed to commercial fishing (Auer 2004). However, population recovery following the collapse has been slow for Lake Sturgeon due to a number of potential factors including blocked migratory paths, habitat degradation and an unusual life history of late maturation and infrequent spawning (Peterson et al. 2007). In Canada, eight designatable units (DUs) have been defined for Lake Sturgeon based on genetic and biogeographical considerations (COSEWIC 2006). Lake Sturgeon populations have been assessed as Special Concern in two DUs, Threatened in one DU and Endangered in five DUs by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2006). In response, a number of government and conservation agencies have developed recovery and management plans for this species (ALSRT 2011; MCWS 2012; SRSMB 2012).

Habitat protection is generally considered of primary importance in sturgeon conservation, though it is difficult to implement (Harkness and Dymond 1961; Waldman and Wirgin 1998; Van Eenennaam et al. 2001; Wilson and McKinley 2004). Hatchery programs to enhance depleted sturgeon populations, including Lake Sturgeon, have become an essential element in recovery efforts (Auer 2004; Pikitch et al. 2005). Analyses of sturgeon population growth using matrix projection models suggest that it is the survival of early life stages that have the greatest effect on overall population growth

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(Gross et al. 2002). Indeed, it has been generally accepted and more recently confirmed that mortality is highest at this stage (Nilo et al. 1997; Caroffino et al. 2010). Therefore, stocking activities are driven by the understanding that loss of critical life history stages may be avoided through release of less vulnerable individuals (Brown and Day 2002). Despite the implementation of stocking programs in fisheries management for over a century, including those for Lake Sturgeon (Harkness and Dymond 1961; Smith and Dingley 1984), the overall effectiveness of these programs remains uncertain. Survival estimates of hatchery-reared sturgeon following release events have been variable due to a number of factors including, but not limited to, gamete collection, rearing environment, size-at-release, and density-dependent effects (Justice et al. 2009; Crossman et al. 2011; Mann et al. 2011). Not unique to Lake Sturgeon stocking programs, Molony et al. (2003) points out that the majority of studies assessing stock enhancement programs have fallen below expectations, but that results are more likely than not associated with poor planning and lack of evaluation. In fact, evaluations of fish stocking programs have been rare in the past, with emphasis placed more on total numbers released (Blankenship and Leber 1995; Bartley 1999; Molony et al. 2003) and political support for stocking programs often remains high despite limited information on overall effectiveness (Fenton et al. 1996).

Information about Lake Sturgeon enhancement programs does exist but has generally focused on the recovery of more southern populations (Schram et al. 1999; Runstrom et al. 2002; Chalupnicki et al. 2011) with limited accounts from similar programs within the northern part of their range. All five Lake Sturgeon designatable units assessed by COSEWIC to be Endangered are represented within the borders of

Manitoba, Canada (COSEWIC 2006) and stocking activity has been a commonly implemented strategy in Lake Sturgeon recovery efforts throughout the province (MCWS 2012). The first account of Lake Sturgeon stocking into provincial waters using artificially propagated individuals was in 1926 at Gull Harbour on Lake Winnipeg (Harkness and Dymond 1961); however, planned release events have been implemented on a more consistent basis since 1994 (MCWS 2012). Stocking activity has primarily occurred in the fall with release of age-0 fingerlings, but improved culture techniques have allowed for an increasing number of age-1 yearling release events (MCWS 2012). Assessment of these stocking events has been rare, and likely a function of inefficient collection methods for young age classes (Benson et al. 2005). Recent advances in juvenile collection procedures (Barth et al. 2009) have allowed for review of artificial propagation programs within the province.

The primary objective of this two-year study was to compare post-release performance (movement and growth) and survival of hatchery-reared age-0 fall fingerlings (FF) and age-1 spring yearlings (SY) from the 2008 Lake Sturgeon year class stocked into the Winnipeg River. Where possible, results were related to length-at-release within stocking events, geographic release location and wild conspecifics in the same reach.

Materials and methods

Study area

Lake Sturgeon stocking assessments were conducted within an impounded area of Manitoba's Winnipeg River between the Slave Falls (50°13'21"N, 95°34'06"W) and Seven Sisters (50°07'09"N, 96°01'03"W) Generating Stations (GS), a stretch of

approximately 40 river km. Following establishment of both facilities in the early 1930s, the river widened in a number of areas creating lake-like environments bounded by in- and out-flow constrictions of fast-flowing water (>1.0 m/s). In this study, 'lake' boundaries were adopted from Barth et al. (2011) and gillnetting effort occurred within the stretch of Numao Lake downstream of Scotts Rapids (4 km long), Nutimik Lake (4 km long), Dorothy Lake (9 km long), Margaret Lake (5 km long), Eleanor Lake (4.5 km long), Sylvia Lake (2 km long), and Natalie Lake (11 km long) (Figure 5.1).

Conditions are known to vary spatially and temporally within this stretch of the Winnipeg River. The depths along the main channel are generally between 10 and 25 m (max. 45 m), and environmental variables differ with distance from the Slave Falls GS. For example, areas upstream of Dorothy Lake have greater water velocities (0.2 to 0.8 m/s) and larger particle sizes (>0.063 mm) than areas downstream of Nutimik Lake, which have lower relative water velocities (<0.2 m/s) and particle sizes (<0.063 mm) (Barth et al. 2011). Flow rates within this river section vary seasonally within a normal range of 500 and 1500 m^3/s, but may exceed these levels in some years despite being heavily regulated. For example, in 2008 and 2009 flow rates reached levels that were among the highest recorded since 1958 (approximately 2400 m^3/s) (Cousins et al. 2012). Wild Lake Sturgeon are present within this reach of the Winnipeg River and, despite being a part of DU5 assessed to be Endangered by COSEWIC (2006), the resident population is considered healthy (Cleator et al. 2010; MCWS 2012). Recent study has shown that the wild juvenile population is more heavily concentrated in the upper reaches (i.e., Numao and Nutimik Lakes) (Barth et al. 2011).

Rearing and marking

Stocked Lake Sturgeon originated from wild adults (8 females, 16 males) collected at an established spawning site within the Winnipeg River directly downstream of the Slave Falls GS. Synchronization of egg collection was facilitated by the use of a commercially available hormonal agent (Ovaprim, Syndel Laboratories Ltd., Vancouver, BC, Canada). The total dose administered to females was based on body mass (0.5 ml per kg) with a priming injection (10% of total dose) followed 12 hours later with a second injection (90% of total dose). Milt was collected opportunistically from males gillnetted on the spawning grounds. Eggs were transported to the Canadian Rivers Institute Field Station near Pinawa, Manitoba (50°08'54"N, 95°55'01"W) on 28 & 29 May, 2008 within two hours of fertilization.

Fertilized eggs were incubated in McDonald hatching jars at a temperature of 12 ± 1 °C. The majority of yolk-sac larvae hatched within nine days following fertilization and they were then transported to the Grand Rapids Fish Hatchery, Grand Rapids, Manitoba (53°09'46"N, 99°16'37"W) prior to first-feeding for grow-out until release. Lake Sturgeon were fed an exclusive diet of live brine shrimp nauplii (*Artemia* spp.; Argent Laboratories, Redmond, WA, USA) for the first month of exogenous feeding then fish were gradually transitioned to a diet of frozen bloodworm (Diptera: Chironomidae; Hikari, Hayward, CA, USA). Feedings were ad libitum. During the summer Lake Sturgeon were reared in a flow-through water system using a blend of well and surface (Cedar Lake, Manitoba) water at a temperature of 17 ± 1 °C. Prior to the fall stocking event, a total of 7,500 Lake Sturgeon fingerlings were divided into three groups and marked at the hatchery by removing the pelvic or anal fin depending on designated

release location (Table 5.1). A subsample of individuals from each release group were measured for total length (TL) to the nearest millimeter using a measuring board and body mass using an electric balance accurate to 0.01 g (Scout II, Ohaus Corporation, Parsippany, NJ, USA) before being implanted with an 8 mm passive integrated transponder (PIT) tag (Biomark, Boise, ID, USA). Tags were placed in the body cavity by way of a mid-ventral incision. Tagged Lake Sturgeon fingerlings had a mean TL of 114.4 ±6.1 mm (±SD) and mean body mass of 5.4 ±0.82 g (±SD). An additional 2,500 fingerling Lake Sturgeon were released into Sylvia Lake but did not receive any mark.

Remaining Lake Sturgeon fingerlings were switched to a water recirculation system on 1 November, 2008 to maintain overwintering temperatures near summer rearing temperatures for continued growth until the spring release. A total of 415 Lake Sturgeon yearlings were available for a spring stocking event and on 14 May, 2009 all individuals were measured for TL and body mass when implanted with a 12 mm PIT tag (Biomark, Boise, ID, USA) in the abdominal cavity as described above. Yearlings were divided into two groups for release into Numao and Dorothy lakes (Table 5.1). Lake Sturgeon yearlings had a mean TL of 244.0 ±16.0 mm and mean body mass of 59.1 ±11.7 g.

Release

Lake Sturgeon fingerlings were released in mid September 2008 into Sylvia, Dorothy, Nutimik and Numao lakes (Table 5.1, Figure 5.1). Fish were transported on the day of stocking in a non-insulated plastic tank during daylight hours approximately 535 km by truck from the Grand Rapids Fish Hatchery to Pinawa, Manitoba (50°09'01"N, 95°52'47"W). Upon arrival, Lake Sturgeon were transferred to a tank assembled on a

pontoon boat and driven to one of the four release sites. Water exchanges en route to the release site provided acclimation to ambient river temperatures. The boat was positioned slightly upstream of the targeted release site and allowed to drift as crew members used nets to fish out the fingerlings and release them into the river. Hatchery-reared individuals were in transport over a 6-10 hour period from the Grand Rapids Fish Hatchery to their release location.

The following spring a similar procedure was undertaken to transport yearlings to the designated release sites on 12 June, 2009 using a custom transport trailer holding two insulated fiberglass tanks. A divider placed within the tank on the pontoon boat allowed both groups to travel to their respective release sites concurrently.

Fish capture and sampling

Post-release information on hatchery-reared Lake Sturgeon was gathered using 25 mm stretched twisted nylon mesh gill nets (Leckie's Lakefish Net and Twine, Winnipeg, Manitoba, Canada) of two to four panels, each measuring 22.9 m long and 1.8 m deep. This mesh size was selected as it has been shown to capture Lake Sturgeon within the targeted size range (<300 mm FL) and minimizes mortality of juvenile Lake Sturgeon and other species (Barth et al. 2009). Nets were bottom-set at various locations along the Winnipeg River from June 14th to October 2nd 2009 and May 11th to October 6th 2010. Gill nets were set overnight and mean (± SD) set duration was 20.5 (± 2.5) hours in 2009 and 23 (± 3.1) hours in 2010. The coordinates of each site were recorded using a handheld GPS unit (Garmin, model #GPS 76, Olathe, Kansas). In both years, catching effort was concentrated at or near the stocking location and these efforts occurred multiple times throughout the field season to account for seasonal changes. Additional

sites were arbitrarily selected in 2009 to survey prospective areas where fish may be found, whereas in 2010, sites were selected based on previous year successes and areas known to support wild Lake Sturgeon in the same impounded stretch of river (Barth et al. 2009; Barth et al. 2011; Henderson, 2013). All Lake Sturgeon captured were checked for a previously applied tag or fin clip. Detection of PIT tags was conducted using a Biomark Pocket Reader (Biomark Inc., Boise, Idaho).

On occasion, hatchery-marked individuals were captured in the gill nets of other studies in the Winnipeg River. Information received from field programs other than the present study was incorporated into analyses where appropriate.

Recapture rate

Catch-per-unit-effort (CPUE, #LKST/100m/24hr) was calculated to standardize information between 1) fall and spring Lake Sturgeon release groups, 2) hatchery-reared and wild Lake Sturgeon, and 3) sampling lakes using the following equation:

CPUE (# LKST/100m/24h) = $\sum$ Lake Sturgeon captured $\div \sum$ Effort x 24 hr,

where *Effort* is expressed as gillnet hours and calculated by taking set duration (in hours), multiplying by the total net length (m), and dividing by 100 m (standardized measure). Only hatchery-reared individuals collected from the gillnetting efforts of this study were included in CPUE calculations.

To account for the different stocking rates of marked hatchery-reared fish (i.e., 7,500 FF vs. 415 SY), 'relative recapture rate' between the two Lake Sturgeon release groups was compared using the following equation (after Brooks et al. 2002):

Relative Recapture Rate = (y_f/Y_f)/(f_e/F_e),

where y_f = number of yearlings stocked in location *f* and later recaptured, Y_f = number of

yearlings stocked in location f, f_e = number of fingerlings stocked in location e and later recaptured, and F_e = number of fingerlings stocked in location e. Relative recapture rate was calculated for each lake when at least one Lake Sturgeon was recovered from both release events (e.g., fall and spring). Thus, relative recapture rates could not be compared for Nutimik Lake because yearlings were not stocked within this lake. All hatchery-reared fish recaptured during the 2009 and 2010 field seasons were included in calculations, including those captured in other study efforts.

Length-frequency distributions were plotted using intervals of 20 mm (e.g., 210-229 mm) for Lake Sturgeon captured in the gillnetting efforts of this study. Incorporated into the plot were the frequencies of hatchery-reared individuals. To clarify, the number of wild, FF and SY in each length interval was divided by the overall number of Lake Sturgeon captured within that study year, regardless of background. Only hatchery-reared individuals collected in the gillnetting efforts of this study were plotted.

To determine if recapture rates of FF and SY were dependent on size at release, the length-at-release for all PIT-tagged individuals recaptured in the Winnipeg River (including other study efforts) were plotted at intervals of 5 mm (e.g., 105-109 mm) and compared to the length-at-release distribution for all PIT-tagged individuals stocked. Two-sample Kolmogorov-Smirnov (K-S) tests were used to compare length-at-release frequencies among stocked and recaptured individuals from fall and spring release events, respectively.

Movement

Site fidelity was assessed by comparing the number of FF and SY that moved through the downstream constriction defining the boundary of the lake where they were

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released with those individuals that did not. A Fisher's Exact Test was used due to small

sample sizes and assumption violations for the Chi-square test.

For all recaptured hatchery-reared Lake Sturgeon in this and other study efforts,

the distance (river km) between recapture and release site was measured using computer

software (Google Earth, version 4.1). Of interest was movement in relation to size at

release, so the initial length-at-release of all recaptured individuals containing a PIT tag

was plotted against the total downstream (- values) or upstream (+ values) distance

moved. Linear regression was used to assess the relationship between length-at-release

and distance moved for all recaptured FF and SY independently.

Growth

Mean total length, body mass and condition of all hatchery-reared Lake Sturgeon

recaptured in 2009 and 2010 were compared between FF and SY using the Mann-

Whitney U test. Condition factor (K) was calculated using the following equation (after

Fulton 1911 *in* Ricker 1975):

$$K_{(TL)} = M \ x \ 10^5 \div TL^3,$$

where M = body mass (g) and TL = total length (mm).

Statistical analyses were completed using SYSTAT (version 9) at a significance

level of $P \leq 0.05$.

Results

During the gillnetting efforts of this study, 238 and 303 sites were sampled across

the Winnipeg River in 2009 and 2010, respectively. Overall, 12 FF and 17 SY were

recaptured and accounted for a very small percentage of the total catch (e.g., 0.37% and

0.46%, respectively). Wild Lake Sturgeon made up 42.5% of the overall catch with all

other species accounting for 56.7% of the overall catch.

Other field programs operating within the same stretch of river in 2008 and 2009 produced an additional 22 FF and 2 SY. Table 5.2 and Table 5.3 summarize the information for all recaptured FF and SY, respectively.

Recaptures

Table 5.4 summarizes the overall CPUE values calculated for Lake Sturgeon in the present study. The number of SY captured during the two-year study was slightly greater (0.04 fish/100m/24h) than for FF (0.03 fish/100m/24h). Regardless, the overall CPUE value for all hatchery-reared fish (0.07 fish/100m/24h) was well below that of wild Lake Sturgeon during the same two-year period (3.7 fish/100m/24h). The highest CPUE value for hatchery-reared Lake Sturgeon was in Numao Lake (0.21 fish/100m/24h) and this was also true for wild Lake Sturgeon (10.0 fish/100m/24h). Interestingly, when assessing the data by release group, SY had the highest overall CPUE value in Dorothy Lake (0.09 fish/100m/24h) whereas the greatest number of FF were recaptured in Numao Lake (0.13 fish/100m/24h).

An unexpected increase in the CPUE values for Lake Sturgeon in Sylvia Lake could suggest that unmarked hatchery-reared individuals were being captured in the gillnetting efforts of this study. However, of the 46 Lake Sturgeon captured in Sylvia Lake over two years, only 4 were within a length interval of other hatchery-reared Lake Sturgeon captured elsewhere (see below). Furthermore, 3 of these 4 individuals had been previously PIT tagged and were part of a study assessing wild juvenile Lake Sturgeon movements following transplantation to Sylvia Lake from other areas along the Winnipeg River (S. Peake, pers. com.).

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Trends associated with recapture rates were quite pronounced when taking into account the different stocking rates between the two release groups. Across all lakes stocked, the relative recapture rate of SY during the two-year study was 23.6 times greater than for FF. In fact, the overall recapture rate of hatchery-reared fish released in Dorothy Lake was 144.2 times greater for SY than FF. For individuals released into Numao Lake the relative recapture rate was 5.5 times greater for SY over FF (Table 5.5).

Hatchery-reared Lake Sturgeon recaptured in the gillnetting efforts of this study were within the length intervals between 230 to 429 mm. In 2009, of the 393 Lake Sturgeon captured, 12.7% of individuals were within this size range (Figure 5.2a). Likewise, of the 1,025 Lake Sturgeon captured in 2010, 12.4% were within this size range (Figure 5.2b). Lake Sturgeon less than 230 mm represented 14.2% and 2.4% of the catch in 2009 and 2010, respectively. In this study the majority of Lake Sturgeon captured were greater than 429 mm and represented 73.0% and 85.2% of the catch in 2009 and 2010, respectively.

Significant differences were not found between the length-at-release frequency distribution of recaptured PIT-tagged FF in comparison to the frequency distribution of all PIT-tagged individuals stocked (Two-sample K-S, $P = 0.264$; Figure 5.3a). In contrast, a significant difference was found between the length-at-release frequency of SY recaptured in comparison to the frequency distribution of all PIT tagged SY stocked (Two sample K-S, $P = 0.038$; Figure 5.3b). However, this discrepancy does not appear to be the result of a skewed distribution (e.g., favouring recapture of large or small individuals).

Movement

Spring Yearlings showed strong site fidelity following release (Table 5.3). In

contrast, 67%, 22% and 21% of all recaptured FF released into Dorothy, Nutimik and

Numao lakes, respectively, had dispersed past river constrictions and into the lake

downstream of their release site. The proportion of FF recaptured in a downstream lake

from that released (10 of 34) was significantly greater than for SY (0 of 10) (Fisher's

Exact Test: P = 0.021).

No significant linear relationship was observed between length-at-release and

river km (rkm) moved, when incorporating both upstream (+) and downstream (-)

direction for previously PIT-tagged hatchery-reared Lake Sturgeon recaptured in this and

other gillnetting efforts (Linear Regression, FF: n = 12, P = 0.79, r^2 = 0.01; SY: n = 17, P

= 0.42, r^2 = 0.04; Figure 5.4).

Growth

Lake Sturgeon released as yearlings had the advantage of continuing their growth

during the winter months. Spring yearlings maintained significantly greater total lengths

during the 2009 and 2010 field seasons, but the difference in body mass was not

significantly different by the end of 2010 (Table 5.6). Despite some discrepancies in size,

the condition (K_{TL}) of FF and SY was not significantly different at any period throughout

the study (Table 5.6).

Discussion

Recovery efforts for threatened and endangered Lake Sturgeon populations have

included the release of hatchery-reared individuals throughout their distribution, but

assessments throughout their northern range are lacking. The primary objective of this

study was to compare the post-release performance of hatchery-reared Lake Sturgeon

from the same year-class stocked into the Winnipeg River, Manitoba, as fall fingerlings

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and spring yearlings. Over a two-year field program relative recapture rates, site fidelity and growth patterns between both release groups were quantified.

Recapture rates for hatchery-reared Lake Sturgeon released as fingerlings and yearlings were low over the two-year study, but relative recapture rate was 24-fold greater in the latter. This was not entirely unexpected and is in line with a number of studies that have found that stocking older, larger fish leads to greater post-release recapture rates than stocking younger, smaller individuals (Hoff and Newman 1995; Salminen et al. 2007; Kampa and Hatzenbeler 2009), including different sturgeon species (Justice et al. 2009; Steffensen et al. 2010; Crossman et al. 2011). It is unclear why more fingerlings were not recaptured in the present study, but several potential reasons are discussed below.

Susceptibility to predation has been shown to increase with decreasing body size (Paradis et al. 1996) and high rates of predation of smaller individuals of other species following stocking events have been reported (Marsh and Brooks 1989; Szendrey and Wahl 1996; Buckmeier et al. 2005). However, the evidence for vulnerability of small sturgeon to predation is equivocal (Gadomski and Parsley 2005a,b; French et al. 2010) and, despite attempts to quantify it, predation of juvenile Lake Sturgeon has yet to be observed at the present study site (Barth et al. 2009). Inadequate energy reserves of small fish, resulting in high overwinter mortality following release, is another potential cause for the reduced recapture rates of fingerlings (Thompson et al. 1991; Sutton and Ney 2001). For instance, temperatures within the Winnipeg River can drop to 1 °C (McDougall, 2011) and the mean size of FF at the time of release (114 mm TL and 5.4 g) appears to be less than wild young-of-the-year (YOY) in the same system where

Henderson (2013) reported that the median size of age-0 Lake Sturgeon captured during fall of 2008 was 154 mm TL and 9.7 g (n = 19). Likewise, the smallest wild-caught Lake Sturgeon in fall and spring gillnetting efforts within this study was 150 mm TL. A similar discrepancy was observed among wild and hatchery-reared Lake Sturgeon in the Wolf River, Wisconsin (Kempinger 1996) and stocking efforts in the Great Lakes have focused on producing Lake Sturgeon fingerlings > 200 mm long in order to improve post-stocking survival (Schram et al. 1999). However, PIT-tag information from recaptured FF revealed that the smallest known hatchery-reared fish to survive the first winter following stocking was released at a size of 105 mm TL (5.0 g). This indicates that the overwintering size threshold, if it exists for juvenile Lake Sturgeon, falls below the mean size of released FF. Gear selection may have favoured the capture of larger individuals (Millar and Fryer, 1999), but this seems unlikely as the 25 mm mesh gill nets used in this study did capture wild Lake Sturgeon individuals as small as 90 mm TL and the greatest number of fingerlings (n = 21, 61.8%) were captured within a two-week period immediately post-release.

Another potential reason for reduced recapture rates of the stocked fingerling fish may have been that this group experienced higher rates of mortality as a result of stress due to transportation and/or limited river time acclimation. However, in a recent study on fingerling-sized Persian Sturgeon, *Acipenser persicus*, plasma levels of glucose, lactate, and cortisol (standard metrics of stress-induced physiological impairment) did not differ between samples taken before and 24 hours after handling and 1.5 hours of transport (Falahatkar et al. 2012). Therefore, while delayed mortality from transport stress such as increased predation or susceptibility to infection or alterations in social behaviour (Brown

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and Day 2002) cannot be discounted, it is unlikely that differences in the ability of fingerlings and yearlings to cope with the stress of handling and transport would have resulted in the observed differences in recapture rates. It is possible that the fish in the present study received an inadequate acclimation period at the release site (< 2 hours), although, this was the same for both fingerlings and yearlings. Results from stream-side rearing studies by Crossman et al. (2011) indicated that the benefits of acclimation may be reduced with increasing age or body size, suggesting that a longer acclimation time for fingerlings in the present study may have improved recapture rates. Clearly further research is required to determine optimal transport and acclimation for stocked juvenile Lake Sturgeon.

Finally, studies of this nature require clear identification of the hatchery fish, especially when wild conspecifics are also present. Tag loss and/or fin regeneration among the FF may have led to underestimated recapture rates in the current study. Preliminary study in 2007 on PIT-tag retention of 8 mm tags inserted into the abdominal cavity of FF (n = 353) indicated low tag loss (1%) within two weeks of the procedure (C. Klassen, unpublished data). However, studies on fin regeneration among individuals within the FF group were not undertaken. Complete fin regeneration was observed in 23% of juvenile Coho Salmon, *Oncorhynchus kisutch*, when at least one-third of the adipose fin was left intact (Thompson and Blankenship 1997). A similar phenomenon may have occurred in this study, particularly with respect to the anal fin mark, as its placement on the body made it difficult to remove the entire fin (C. Klassen, pers. obs.) and none of these marks were observed in 2009 or 2010 gillnetting efforts. Interestingly, the frequency of unmarked and presumed wild Lake Sturgeon captured within the 230 to

429 mm TL interval (i.e., hatchery fish sizes) was high over the two-year gillnetting program (n = 198). Although it is plausible that some of these individuals were misidentified hatchery-reared fish, a large number of age-0 Lake Sturgeon were captured in the same stretch of river during the spring and summer prior to the 2008 fall stocking event (Barth 2011; Henderson 2013). As such, it may be more plausible that FF were required to compete with what was determined to be a strong naturally produced 2008 year-class (Barth 2011). For instance, Laarman (1978) determined that Walleye, *Sander vitreus*, stocking programs were only 5% successful when supplementing natural year-classes in comparison to 48% successful when introducing hatchery-reared fish to lakes with no previously existing natural population.

There are cases in the literature where stocking different sized hatchery fish has been met with mixed results and these results have been attributed to annual variability or differences among release locations (Brooks et al. 2002; Saito et al. 2011). Interestingly, stocking location does appear to have greatly influenced relative recapture rates among the fingerlings and yearlings released in this study as the difference was 144 times greater in Dorothy Lake versus only 5.5 times greater in Numao Lake. The CPUE values for SY were relatively similar between the two lakes, while the CPUE value of FF was higher in Numao Lake than Dorothy Lake. The specific environmental advantages Numao Lake provided to fingerlings is unclear. Interestingly, Jennings et al. (2005) found that hatchery-reared Walleye did the best in lakes that also supported wild conspecifics. Similarly, high concentrations of wild juvenile Lake Sturgeon are found in Numao Lake (Barth 2011). In fact, of the 71 unmarked Lake Sturgeon < 230 mm TL captured in the gillnetting efforts of this study, 53 (74.6%) were located in Numao Lake, in contrast to

just a single individual (1.4%) in Dorothy Lake.

Justice et al. (2009) suggested that density-dependent factors affected the survival of juvenile sturgeon at sizes < 250 mm but this would not appear to be the case in our system where densities of wild juveniles are greatest in Numao Lake. It could be hypothesized that the FF released into Numao Lake benefited from higher Lake Sturgeon densities as wild juveniles are known to congregate in deep waters within this river system (Barth et al. 2009) and lab studies have shown physiological benefits from being in the presence of conspecifics (Allen et al. 2009). If true, competition between existing and recently released individuals may not be occurring, as earlier suggested, or may be dependent on a density threshold. Further research on the ability of hatchery-reared Lake Sturgeon to integrate into established populations (of wild or hatchery origin) would provide additional information with which to make stocking decisions.

In regard to the importance of considering site selection of stock enhancement, SY from the present study were found to have greater site fidelity following release as all individuals were recaptured in the same lake they were stocked. Not only does this represent an advantage when stocking programs are trying to target specific locations but is representative of behaviour observed among wild juveniles from the same population. For example, only 6 of 714 (0.8%) recaptured wild juvenile Lake Sturgeon were found to move through downstream lake boundaries over a three-year period in the same river system (Barth et al. 2011). In contrast, 10 of 34 (29%) FF from this study were recaptured within a reach of the Winnipeg River downstream of their release lake. The furthest known distance moved by a hatchery-reared sturgeon in this study (10.3 rkm) occurred within 5 days post-release following the fall stocking event and 5 of 21 (24%) FF

captured within 12 days post-release had moved >4 rkm downstream. This distance was not observed for released SY at any point and is a rare occurrence among wild juveniles in the same river system (Barth et al. 2011). It is unknown if the downstream movements among FF were volitional or not. Post-stocking dispersal has been attributed to a number of reasons including chronic stress associated with release activities (Mueller et al. 2003), poor swimming abilities (Crossman et al. 2011) and search for suitable habitat (Secor et al. 2000; Trested et al. 2011).

Closer examination of the movement information for FF by lake shows that site fidelity was greater among individuals released into Numao Lake (15 of 19, 79%) than Dorothy Lake (2 of 6, 33%). Oldenburg et al. (2011) also found that release habitat was the most influential factor affecting post-release dispersal of juvenile Pallid Sturgeon, *Scaphirhynchus albus*, even when some fish were acclimated to increased water flows. The reasons why FF were more inclined to stay within Numao Lake is again unknown, but, given the high concentrations of juvenile Lake Sturgeon located in the same area, it is likely a reflection of preferred habitat. However, critical swimming speeds (U_{crit}) for Lake Sturgeon within the size range of the FF released in this study were estimated to be 0.31 m/s (Peake 2004) and some areas of the Winnipeg River (e.g., main channel and channel margins) are known to exceed this velocity (Barth et al. 2009). Greater rates of upstream movement by released yearlings over the two-year study than FF suggests that the FF may have struggled to navigate the river, given their smaller size. Closer proximity to areas known to have slower flows in Numao Lake (e.g., back bays) may have provided some refuge for released FF post-release and thereby reduced downstream dispersal.

Yearlings were larger, both in total length and body mass, than fingerlings at the point of release and this size advantage persisted over the first year. By the second year, differences in total length were weakly significant and body mass was not significantly different among the age-2 hatchery fish. Growth convergence between fish stocked at different ages/sizes after several years following stocking has been observed in other species (Pratt and Fox 2003; Amtstaetter and Willox 2004). The largest individual captured in the second year of gillnetting was a FF. The growth of this large FF may be related to location, as it was the only hatchery-reared fish captured in Eleanor Lake during the final study year. The wild Lake Sturgeon population of this river system has also displayed increased growth rates among lakes downstream of Numao Lake and this is thought to be a function of reduced sturgeon densities (Barth 2011). As such, it would appear that FF have the capacity for high growth rates provided optimal foraging opportunities. Body condition (K_{TL}) was also not significantly different between the two release groups in either year following stocking. In fact, all the hatchery-reared fish displayed mean conditions (e.g., 0.35 to 0.41) that were comparable (e.g., 0.36 to 0.41) to those reported for wild Lake Sturgeon in the same river system of similar sizes (e.g., 250 to 349 mm TL) (Barth 2011).

Assessment of stocking programs in relation to size generally focuses on large-scale differences most often associated with different ages. Growth rate variability within the same year-class is often high in sturgeon culture environments (Nathanailides et al. 2002; Chapter 2) and this fine-scale variability could potentially have an impact on post-release performance. The secondary objective of this study was to assess size-at-release in relation to post-stocking performance of fingerling and yearling release events,

respectively.

Contrary to expectation, size variability within the FF and SY release groups did little to predict the performance of individuals following release. Recaptured FF and SY were not representative of just the largest individuals released in the fall and spring stocking events, respectively. This result contrasts with that from a similar assessment of White Sturgeon by Justice et al. (2009) where recapture frequencies clearly favoured the larger individuals stocked. Discrepancies may be due to the range of sizes being assessed. For instance, the study by Justice et al. (2009) had a length distribution spanning approximately 350 mm. In comparison, the size range was much lower among FF (e.g., 69 mm) and SY (e.g., 104 mm) of this study and perhaps an insufficient range of sizes to detect length-at-release effects. Overwinter detection of juvenile Lake Sturgeon was also not related to fish size (Crossman et al. 2009) but, as in our study, the size range of study fish was smaller.

Length-at-release within stocking events have been shown to influence age-0 Lake Sturgeon movements (Crossman et al. 2011) but did not appear to have an effect on distance moved when assessing the FF or SY release groups of this study. However, the former study was looking at movement within a 24-hour period, whereas, the present study was assessing movements beyond this time window. As such, the effects of length-at-release on movement may be limited to very short periods post release. Interestingly, no relationship was reported among wild Lake Sturgeon juveniles of variable sizes in the Winnipeg River when assessing distance between initial capture and subsequent recapture (Barth et al. 2011).

In conclusion, stocking yearling Lake Sturgeon into the Winnipeg River resulted

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in higher relative recapture rates and site fidelity than fingerlings throughout a two-year period post-release. However, the extent to which SY outperformed FF depended on location, highlighting the need for site-specific assessments and decision-making, a sentiment endorsed following other reviews of stock enhancement programs (Brooks et al. 2002; Pratt and Fox 2003; Leber et al. 2005). The results of this study also indicated that the advantages of greater body size are limited to large-scale differences associated with age and are not evident for fine-scale differences observed among fish of the same age. However, the present study design could not disentangle size from age or season effects. The results of this study should be considered cautiously as they represent the performance of a single year-class over a relatively short assessment period. In addition, the stocking event assessed could be considered supplementary in nature, as natural recruitment was present. Results, particularly those associated with recapture rates, may have been different if the study utilized a stretch of river where natural recruitment is not known to occur or is reduced. Conveniently, the wild Lake Sturgeon of this stretch of river are well studied and provided an opportunity to compare the performance of hatchery-reared sturgeon with that of wild conspecifics in the same system. It was observed that FF utilized known nursery areas in Numao Lake, SY actively moved to upstream areas in Dorothy Lake and fish were recaptured with body condition comparable to similarly-sized wild Lake Sturgeon. These data provide encouraging signs that hatchery-reared individuals can contribute to recovery efforts.

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Table 5.1 Summary of Lake Sturgeon groups released into the Winnipeg River, Manitoba. Information not applicable to some groups is indicated by n/a.

Lake Released	Number Released	Date Released	Date(s) Tagged	Fin Clip Applied	Number PIT tagged
Fall Fingerlings					
Numao	2,500	17-Sep-08	15-Sep-08	Left Pelvic	631
Nutimik	2,500	16-Sep-08	14-Sep-08	Anal Fin	633
Dorothy	2,500	15-Sep-08	12 to 14-Sep-08	Right Pelvic	632
Sylvia	2,500	14-Sep-08	n/a	n/a	0
Totals	**10,000**				**1,896**
Spring Yearlings					
Numao	207	12-Jun-09	14-May-09	n/a	207
Dorothy	208	12-Jun-09	14-May-09	n/a	208
Totals	**415**				**415**

Table 5.2 Information for hatchery-reared Lake Sturgeon released as fingerlings in three locations along the Winnipeg River, Manitoba and recaptured over a two year period.

Stocking Data			Recapture Data							
Lake	TL (mm)	Mass (g)	Date	Lake	RKM[1]	TL (mm)	Mass (g)	Age (days)	Mark/ Tag[2]	Data Source[3]
Numao	115	5.70	19-Sep-08	Numao	-2.05	116	5.4	106	LP;PIT	*L.M.H*
			19-Sep-08	Numao	-2.05	115	5.0	106	LP	*L.M.H*
			19-Sep-08	Numao	-2.05	117	5.3	106	LP	*L.M.H*
			19-Sep-08	Nutimik	-4.35	105	2.5	106	LP	*C.C.B*
	120	6.10	23-Sep-08	Numao	-1.10	134	3.6	110	LP; PIT	*L.M.H*
	131	8.03	23-Sep-08	Numao	-1.10	147	4.5	110	LP; PIT	*L.M.H*
			23-Sep-08	Numao	-1.10	135	3.5	110	LP	*L.M.H*
			23-Sep-08	Numao	-1.10	131	3.1	110	LP	*L.M.H*
			1-Sep-09	Numao	-0.90	270	51.2	453	LP	
	115	6.1	29-Sep-09	Numao	-1.92	278	78.0	481	LP; PIT	
			30-Sep-09	Numao	-2.15	236	45.0	482	LP	
	116	6.0	9-Jun-10	Numao	0.29	272	101.0	734	LP; PIT	
	108	5.7	10-Jun-10	Numao	-0.31	280	105.0	735	LP; PIT	
			6-Jul-10	Nutimik	-4.93	244	55.0	761	LP	
	125	6.8	7-Jul-10	Nutimik	-5.01	281	78.0	762	LP; PIT	
			22-Jul-10	Numao	0.35	255	53.0	777	LP	
	105	5.0	24-Aug-10	Numao	-0.28	281	90.0	810	PIT	
			25-Aug-10	Numao	-0.58	324	124.0	811	LP	
			10-Sep-10	Nutimik	-4.29	365	219.0	827	LP	
Nutimik			18-Sep-08	Nutimik		115		105	AF	*C.C.B*
			19-Sep-08	Nutimik	-0.37	119	3.9	106	AF	*L.M.H*
			19-Sep-08	Nutimik	-0.37	115	3.3	106	AF	*L.M.H*
	113	5.47	19-Sep-08	Nutimik	-0.37	113	2.7	106	AF; PIT	*L.M.H*
			19-Sep-08	Nutimik	0.34	113	3.3	106	AF	*C.C.B*
			19-Sep-08	Nutimik	0.34	113	3.4	106	AF	*C.C.B*
			19-Sep-08	Nutimik	0.34	112	3.6	106	AF	*C.C.B*
	112	5.20	23-Sep-08	Dorothy	-7.72	121		110	AF; PIT	*L.M.H*
	110	5.17	13-Jul-09	Dorothy	-7.70	195	31.6	403	AF; PIT	*S.J.P*
Dorothy			19-Sep-08	Dorothy	-0.74	111	3.2	106	RP	*L.M.H*
			19-Sep-08	Dorothy	-0.74	111	3.3	106	RP	*L.M.H*
			20-Sep-08	Eleanor	-10.32	125	3.8	107	RP	*C.C.B*
			26-Sep-08	Margaret	-7.13	124	4.2	113	RP	*C.C.B*
	112	4.60	26-Sep-08	Margaret	-7.13	114	2.9	113	RP; PIT	*C.C.B*
			10-Aug-10	Eleanor	-7.91	411	315	796	RP	

[1] Upstream (+) and downstream (-) distance moved (river km) between release and recapture site

[2] LP = Left-Pectoral; AF = Anal Fin; RP = Right-Pectoral; PIT = Passive Integrated Transponder Tag

[3] *L.M.H.* = Laura Henderson; *C.C.B.* = Cameron Barth; *S.J.P.* = Stephan Peake

Table 5.3 Information for hatchery-reared Lake Sturgeon released as yearlings in two locations along the Winnipeg River, Manitoba and recaptured over a two year period.

Stocking Data			Recapture Data						
Lake	TL (mm)	Mass (g)	Date	Lake	RKM[1]	TL (mm)	Mass (g)	Age (days)	Data Source[2]
Numao	225	46.14	3-Sep-09	Numao	-2.08	292	94	455	
	243	53.79	29-Sep-09	Numao	-1.20	332	127	481	
	240	50.15	9-Jun-10	Numao	0.09	329	170	734	
	252	68.20	10-Jun-10	Numao	-0.34	294	124	735	
	241	53.44	21-Jul-10	Numao	-1.20	348	156	776	
Dorothy	257	75.86	9-Jul-09	Dorothy	1.04	288		399	*S.J.P*
	202	38.60	10-Jul-09	Dorothy	1.04	235		400	*S.J.P*
	246	56.03	17-Jul-09	Dorothy	0.67	292	93	407	
	267	80.99	20-Aug-09	Dorothy	-2.80	332	143	441	
	252	56.70	20-Aug-09	Dorothy	-2.56	316	109	441	
	233	45.84	25-Aug-09	Dorothy	0.26	303	95	446	
	257	65.50	25-Aug-09	Dorothy	0.18	321	115	446	
	246	55.42	26-May-10	Dorothy	1.81	346	150	720	
	239	58.10	26-May-10	Dorothy	1.81	335	128	720	
	263	68.90	27-May-10	Dorothy	1.73	356	169	721	
	234	47.89	25-Jun-10	Dorothy	1.76	373	212	750	
	234	50.30	25-Jun-10	Dorothy	2.35	330	155	750	

[1] Upstream (+) and downstream (-) distance moved (river km) between release and recapture site

[2] *S.J.P.* = Stephan Peake

Table 5.4 Catch-per-unit-effort (CPUE) of wild and hatchery-reared Lake Sturgeon (FF: fall fingerlings, SY: spring yearlings) over a two-year gillnetting program in the Winnipeg River, Manitoba.

| | Gill Nets | | WILD LKST | | HATCHERY LKST | | | | | |
Lake	Duration	Effort	Total No.	CPUE (#LKST/100m/24hr)	FF No.	CPUE (#LKST/100m/24hr)	SY No.	CPUE (#LKST/100m/24hr)	Total No.	CPUE (#LKST/100m/24hr)
Numao	2010.39	1500.82	627	10.027	8	0.128	5	0.080	13	0.208
Nutimik	2646.75	1964.66	623	7.610	3	0.037	0	0.000	3	0.037
Dorothy	3389.64	2569.79	63	0.588	0	0.000	10	0.093	10	0.093
Margaret	801.08	644.17	8	0.298	0	0.000	0	0.000	0	0.000
Eleanor	1481.65	1103.98	24	0.522	1	0.022	0	0.000	1	0.022
Sylvia	1250.96	944.31	46	1.169	0	0.000	0	0.000	0	0.000
Natalie	324.59	271.22	0	0.000	0	0.000	0	0.000	0	0.000
Total	11905.06	8998.95	1391	3.710	12	0.032	15	0.040	27	0.072

Table 5.5 Relative recapture rate between fall fingerlings (FF) and spring yearlings (SY) over the 2009 and 2010 study years across release locations.

Year(s)	Lake	Released FF No.	Recaptured FF No.	Recapture Rate	Released SY No.	Recaptured SY No.	Recapture Rate	Relative Recapture Rate
2009								
	Numao	2500	3	0.0012	207	2	0.0097	8.05
	Nutimik	2500	1	0.0004	0	*n/a*	*n/a*	*n/a*
	Dorothy	2500	0	0.0000	208	7	0.0337	*n/a*
	TOTAL	**7500**	**4**	**0.0005**	**415**	**9**	**0.0217**	**40.66**
2010								
	Numao	2500	8	0.0032	207	3	0.0074	2.30
	Nutimik	2500	0	0.0000	0	*n/a*	*n/a*	*n/a*
	Dorothy	2500	1	0.0004	208	5	0.0123	30.64
	TOTAL	**7500**	**9**	**0.0012**	**415**	**8**	**0.0193**	**16.06**
Overall								
	Numao	2500	11	0.0044	207	5	0.0242	5.49
	Nutimik	2500	1	0.0004	0	*n/a*	*n/a*	*n/a*
	Dorothy	2500	1	0.0004	208	12	0.0577	144.23
	TOTAL	**7500**	**13**	**0.0017**	**415**	**17**	**0.0410**	**23.63**

n/a = not applicable

Table 5.6 Total length, body mass and condition factor comparisons between fall fingerlings (FF) and spring yearlings (SY) during the 2009 and 2010 study years. Bolded values indicate significant differences at $P \leq 0.05$.

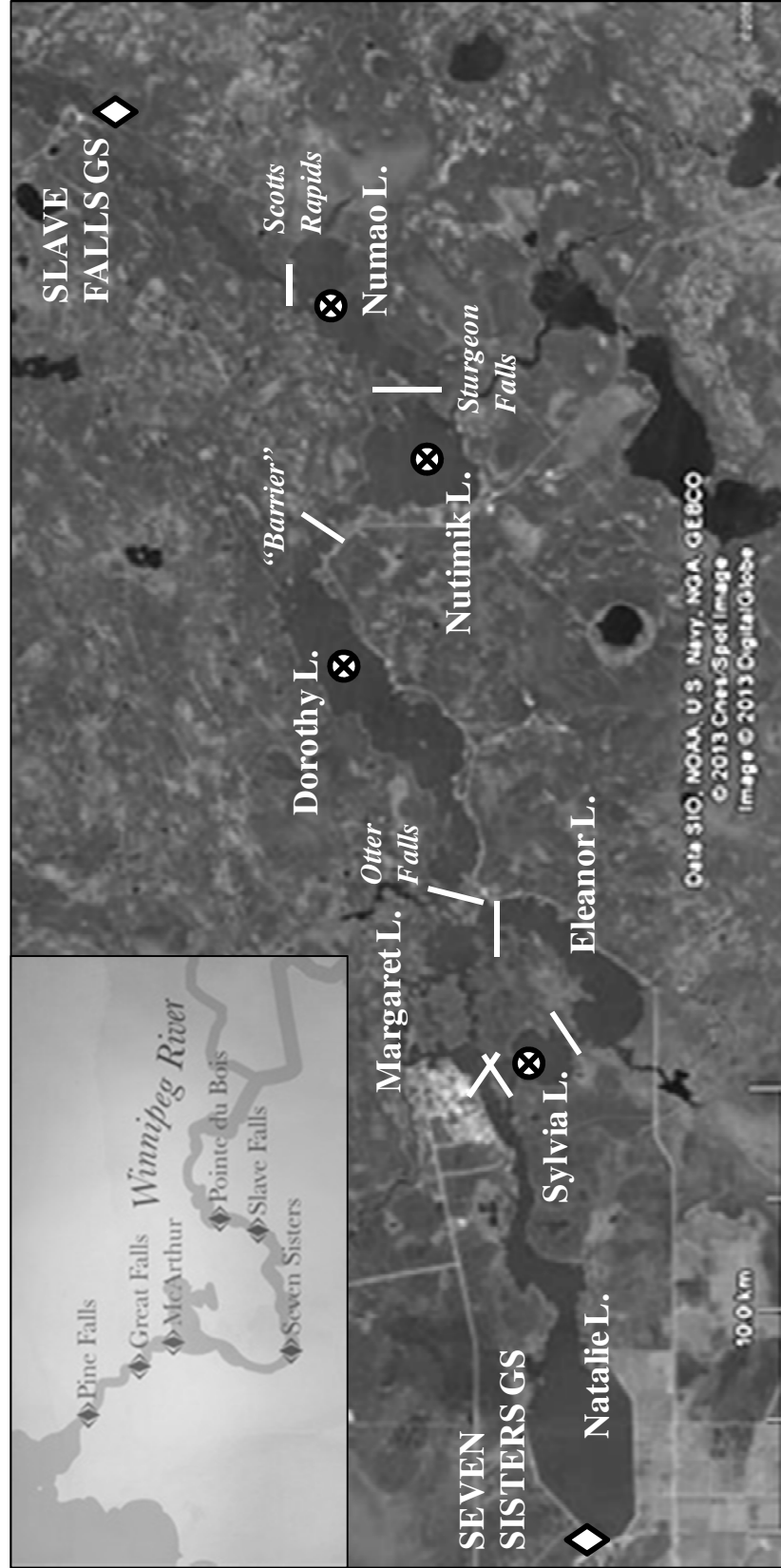| Variable	Year	Group	N	Mean	SD	Mann-Whitney U	P =
TL	2009	FF	4	244.75	37.84		
(mm)		SY	9	301.22	30.08	3.0	**0.02**
	2010	FF	9	301.44	54.97		
		SY	8	338.88	23.29	16.0	**0.05**
Mass	2009	FF	4	51.45	19.50		
(g)		SY	7	110.53	18.99	< 0.001	**0.01**
	2010	FF	9	126.67	86.17		
		SY	8	158.00	27.55	16.5	0.06
Condition	2009	FF	4	0.348	0.069		
(K_{TL})		SY	7	0.359	0.020	12.0	0.71
	2010	FF	9	0.412	0.063		
		SY	8	0.407	0.055	38.0	0.85

Figure 5.1. Study area between the Slave Falls and Seven Sisters Generating Station. Insert shows orientation with respect to four other generating stations along the Winnipeg River within the borders of Manitoba. Lake boundaries are defined after Barth et al (2011). The symbol ⊗ indicates Lake Sturgeon release locations. Insert from http://www.lwcb.ca/

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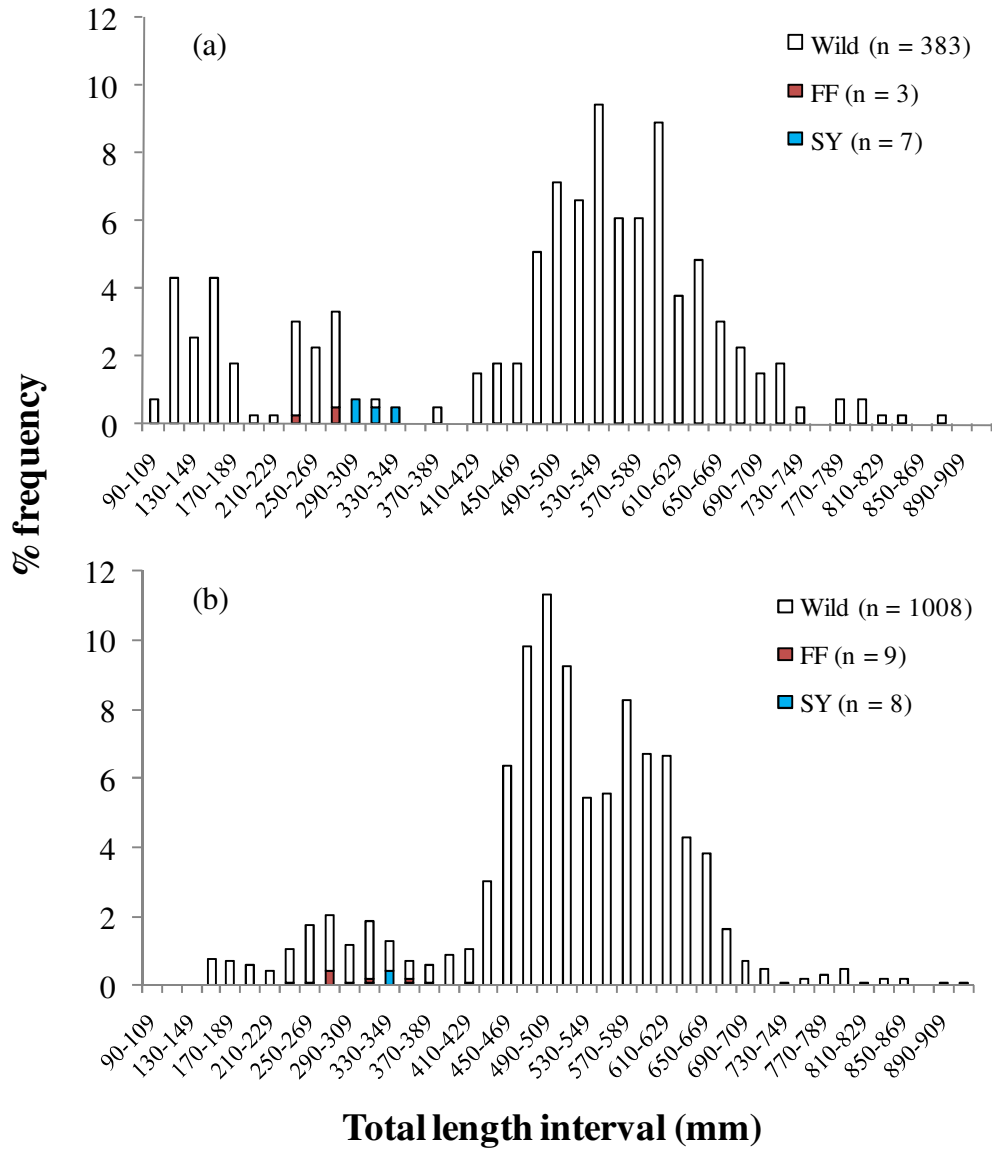Figure 5.2 Total length (mm) frequency histograms (20 mm intervals) of juvenile Lake Sturgeon captured in 25 mm mesh gill nets set in the Winnipeg River, Manitoba during (a) 2009 and (b) 2010.
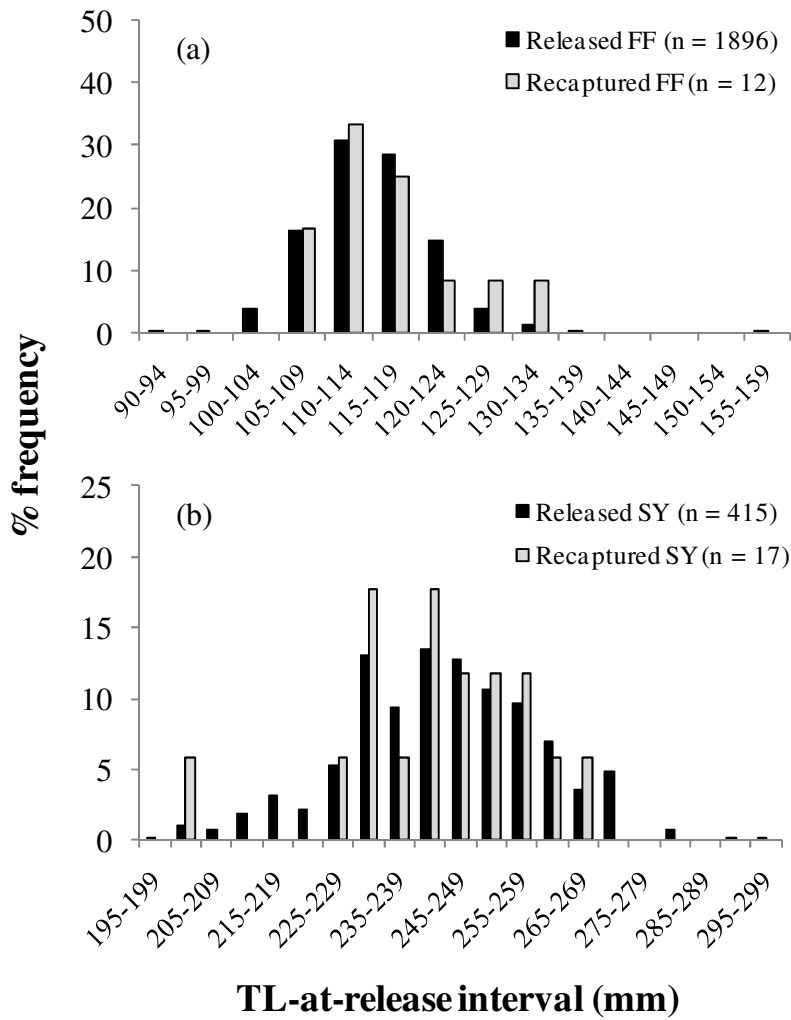
Figure 5.3 Length-at-release distributions for (a) fall fingerlings (FF) and (b) spring yearlings (SY) released into the Winnipeg River, Manitoba and subsequently recaptured over a two year period post-release.
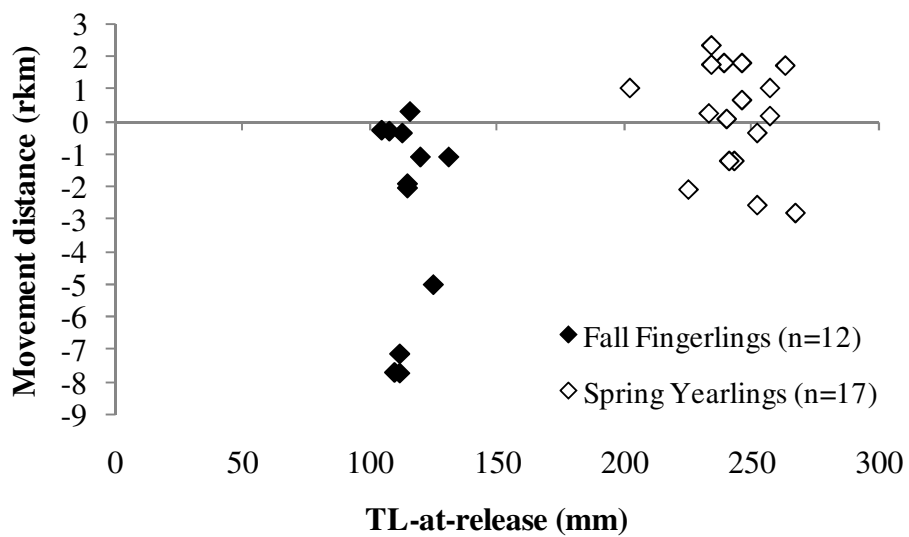
Figure 5.4 Scatterplot of the distance moved (rkm) by Lake Sturgeon fall fingerlings (FF) and spring yearlings (SY) recaptured in the Winnipeg River, Manitoba during 2009 and 2010 as it related to total length-at-release (mm). Positive and negative values indicate upstream and downstream movement, respectively.

Chapter 6

General Discussion

Research overview

Causes of growth and size variability

The first objective of this study was to determine the cause(s) of growth and size variability among Lake Sturgeon cohorts. Size divergence, most often mediated through variable growth rates, has been observed within sturgeon cohorts (Gisbert et al. 2000; Nathanailides et al. 2002), including Lake Sturgeon as described in this thesis. However, this study is, to the best of my knowledge, the first attempt at determining an underlying cause in Lake Sturgeon. Among all fish species, higher growth rates and larger sizes have traditionally been associated with increased fitness. Factors that are likely to select for high growth rates include energetic demands of migration, short growing seasons prior to winter, competitive advantages and predation refuges (Arendt 1997). However, persistence of individuals with lower growth rates and smaller sizes has been observed (Pfister and Stevens 2002) and has been explained through tradeoffs with higher growth rates including compromised antipredator behaviour, somatic development, immune function and responses to physiological stressors (Arendt 1997; Mangle and Stamps 2001).

Initial studies examined the potential causes of growth/size variability and if they were the result of inherent (e.g., genetics) or extrinsic (e.g., environment) factors (Ch.2). The experimental design was fashioned after studies conducted on the same topic using juvenile cichlids by Koebele (1985) and included apparatus allowing for group and isolated rearing environments among larval Lake Sturgeon. Comparisons were made using the coefficient of variation (CV) for total length, where larger CV values indicate greater size variability. It was hypothesized that if growth rates in Lake Sturgeon are

influenced more by genetic make-up then size variability among individuals reared in isolation would be equal to (or greater than) those individuals reared in group environments. Results confirmed that inter-individual difference in size among cohort members was greater when reared in groups versus isolated rearing environments supporting the idea that growth/size variability is not the result of an underlying fixed genotype but rather of phenotypic plasticity dependent on rearing environment. Furthermore, similar outcomes across multiple family groups produced from a single male and female, respectively, suggests that the environmental influences of growth/size variability transcend family background.

Two additional environmental parameters were incorporated into lab studies assessing inherent versus extrinsic mechanisms leading to growth/size variability and included resource level and social interaction (e.g., psychological stress). Results showed that CV values were greater among individuals provided half as much food as neighbouring groups. In addition, research was conducted such that groups of juvenile Lake Sturgeon were isolated only during feeding events and these groups showed no significant difference in CV values in comparison to groups having been permanently isolated. Together, these results suggest that access to feed is the primary driver of growth/size variability with some individuals being better able to acquire resources than others. As such, this study supports the disproportional food acquisition hypothesis proposed by Magnuson (1962) to explain size divergences over time.

Follow-up experiments were undertaken to determine if size-independent (i.e., behavioural phenotype) or size-dependent (i.e., relative size) factors could best explain why some individuals may be acquiring more feed than others leading to size divergence

within groups (Ch. 3). Experiments were conducted under the framework of an unequal competitors ideal free distribution (IFD) (Sutherland and Parker 1985) using experimental apparatus developed by Abrahams (1989). Under this scenario, the more competitive individuals are predicted to be distributed within the most profitable feeding patch. Study groups included juvenile Lake Sturgeon that consisted of 1) size-matched individuals having different growth backgrounds (e.g., fast and slow) and 2) individuals of different sizes (large and small). It was hypothesized that if interactions were driven by underlying behavioural types, then both size-matched individuals previously determined to be fast-growers and fish of larger relative size would monopolize the most profitable feeding patches. Interestingly, study groups did not conform to an ideal free distribution (Fretwell and Lucas 1970), let alone show monopolization of foraging patches by any one group. This may be the result of using experimental apparatus designed for visual feeders, where Lake Sturgeon are driven more by olfaction during foraging (Kasumyan 2002), although there is some evidence that even wild Lake Sturgeon may not conform to an IFD in relation to food availability (Barth 2011).

There are a number of factors that may have compromised the results of this study in Chapter 3. Individuals used in the current study were well-fed prior to and during experimentation. In addition, the current study was conducted approximately 6 months following the initial study assessing inherent versus extrinsic factors on growth rate when juvenile Lake Sturgeon were much smaller. As such, feeding motivation may not have been sufficient to answer questions related to competitive asymmetries. It is suggested that future studies look at specific feeding interactions at earlier stages in development, under reduced feed and over a longer duration. For instance, it would be extremely

interesting to follow size-matched individuals of past fast- and slow-growing backgrounds to determine if size divergence is repeatable (e.g., past fast/slow-growers are again fast/slow-growers). Until such a study is completed, the influence of inherent factors during competitive interactions cannot be entirely discounted.

Studies conducted in Ch.2 and Ch.3 did not definitively determine a link between growth rate and size with underlying inherent mechanisms. As such, the notion that Lake Sturgeon life-history is driven by a 'bet-hedging' strategy comprised of many offspring with different fixed characteristics remains unsubstantiated. However, experiments could also not conclusively determine if size-dependent factors were any more of a factor during foraging events. Competition for resources is just one of many potential extrinsic influences fish may encounter, and one expected to be exaggerated under the typically high rearing densities maintained in aquaculture environments. In addition to further study on this topic, it is strongly suggested that future studies assess the consequences of growth rate and size variability of Lake Sturgeon under additional extrinsic factors including predation threats, virus challenges, and temperature extremes.

Consequences of growth and size variability

The persistence of intra-cohort growth and size variability is linked to the consequences associated with being a fast/slow-grower or large/small individual. As such, the second objective of this study was to try and determine how differences in body size may influence potential recruitment. Strong year-classes have been shown to be linked with overwinter survival among cohort members in other species (Post and Evans 1989; Hurst and Conover 1998). Therefore, lab experiments incorporating relatively large and small individuals were undertaken to determine how size affected the ability of

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juvenile Lake Sturgeon to endure an extended (i.e., 2 months) low water temperature challenge (Ch.4). Groups of large and small individuals were sampled following 1) a 3-week acclimation period, 2) a temperature decrease from 16.5 to 4 °C which occurred over a 3-week period, 3) 4 weeks at 4 °C, 4) 8 weeks at 4 °C and 5) a temperature increase from 4 to 16.5 °C which occurred over a 3-week period. A lack of replication and low sample sizes made analysis and interpretation difficult, but some interesting trends did emerge. Unexpectedly, the mean body condition (K_{FL}) of smaller individuals was not significantly lower than larger conspecifics having experienced the same temperature reduction. Feedings to satiation during the acclimation period (i.e., 10% BM daily), combined with continued feedings (i.e., 1% BM every other day) offered throughout the two-month low temperature challenge appears to have been more than adequate in sustaining fish nutritionally, as resting metabolic rates are also greatly reduced in cold environments (Gillooly et al. 2001). Resting metabolic rates are also influenced by body size (Gillooly et al. 2001); however, there was no evidence that the large and small individuals were responding to the reduced temperatures and feeding rates differently as indicated by significantly similar levels of plasma glucose and triglyceride levels throughout the low temperature challenge.

Plasma glucose levels increased in fish immediately following changes in temperature, a metabolite known to be influenced by acute stress events (Mazeaud et al. 1977). Mortality was also not found to be significantly different among large and small fish, nor was there any mortality during or following the two-month period at 4ºC. It was found that overall activity rates decreased significantly at 4 °C in comparison to temperatures of 16.5 °C, although feeding continued throughout the two-month period.

As such, it would appear that Lake Sturgeon juveniles were able to adapt to the cold water environments imposed on them in this study to some degree. Given that the conditions of this experiment did not represent the winter temperatures experienced by wild conspecifics (e.g., 1 °C) (McDougall 2011), results should be interpreted cautiously. Additional study under lower temperatures and feed should be undertaken to better determine if an overwintering size threshold exists for young-of-the-year Lake Sturgeon.

Laboratory experiments provide the benefit of having highly controlled environments, but rarely represent natural conditions. As such, the final experiment in this study was to assess the performance of hatchery-reared Lake Sturgeon released into the Winnipeg River, Manitoba as age-0 fall fingerlings (FF) and age-1 spring yearlings (SY) (Ch.5). Fisheries enhancement programs have generally focused on total numbers stocked (Molony et al. 2003) and release groups consisting of older, larger individuals, which have been shown to have greater survival (Justice et al. 2009; Steffensen et al. 2010). However, the concept of releasing hatchery-reared fish that represent, as closely as possible, individuals that are naturally produced is emerging in conservation biology (Brown and Day 2002). In order to determine if size variability persists under natural conditions, a large number of Lake Sturgeon from each release group were tagged with passive integrated transponder (PIT) tags following measurements (e.g., FF = 1890, SY = 415). Over a two-year gillnetting study it was determined that, although size associated with the different release groups (e.g., age-0 vs. age-1) did impact the overall results, intra-individual differences in size persisted in the river over time across both release events. In addition, movement could not be related to size-at-release.

Studies conducted in Ch.4 and Ch.5 showed that size variability can and does

persist within juvenile Lake Sturgeon cohorts. As such, the 'bigger is better' hypothesis (Miller et al. 1988; Litvak and Leggett 1992) was not supported in the present study. However, all individuals used in the present study were artificially produced (i.e., hatchery-reared) and field studies to assess growth/size variability within wild Lake Sturgeon cohorts are needed to put these results into context. Until such studies are completed, it is advised that both slow-growing and small individuals continue to be integrated into Lake Sturgeon recovery programs. In addition, periodic gillnetting programs along the Winnipeg River are encouraged to assess longer-term performance of the released 2008 Lake Sturgeon cohort in relation to size-at-release.

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