STAGE STRUCTURE MUST INFORM RECOVERY IN FISH POPULATIONS: A CASE FOR LAKE STURGEON IN THE NAMAKAN RIVER, ONTARIO

Thesis Presented to the Lakehead University Faculty of Natural Resources Management
in Partial Fulfillment of the Requirements of a Ph.D. in Forest Sciences

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April 2018

Acknowledgements

This project was made possible by funding from the Ontario Ministry of Natural Resources and Forestry's Species at Risk Stewardship Fund, as well as the Rainy Lake Conservancy, in conjunction with Voyageur's National Park Association, the Quetico Foundation, and the Natural Sciences and Engineering Research Council.

Field work was conducted with additional support from the Ontario Ministry of Natural Resources and Forestry, Voyageurs National Park, the Minnesota Department of Natural Resources, the US Department of Agriculture Forest Service, Quetico Provincial Park, the Quetico Foundation, and the Rainy Lake Conservancy.

Field work was made possible with help from Lakehead University interns: Michelle Desaulniers, Sarah Schroeder, Samuel Pegg, and Kaylee Busniuk; volunteers: Dan Brazeau, Steve Purves, Pete Gammond, Allison Bannister, Greg Toombs, Jon Kivinen, Megan Clark, Endre Lukacs; undergraduate thesis students: Justine Tessier, Amanda Suttie, and Blair McNaughton; and Quetico Foundation interns: Hannah Geherels, Leith Reilly, Claire Farrel, Lucas Paulson, and Shahin Muttalib.

Special thanks to my advisors, Brian McLaren and Gregory Pyle; and my committee members, Tim Haxton and Steven Chipps.

Disclaimer: Some of the information contained within this document is covered by a non-disclosure agreement between Lakehead University, the Lac La Croix First Nation, and the Ontario Ministry of Natural Resources and Forestry. This information will be removed from the publicly available versions of this document.

Abstract

Lake sturgeon are a large bodied, slow maturing, intermittently reproducing acipenserid native to central North America. The species is a conservation concern range-wide because of population declines during the 19th and 20th centuries related to overharvest and habitat degradation. It is generally accepted that harvest limitations alone are not enough to recover the species, but a stock-recruitment model accounting for the effect of the species' complex, partially migratory life history has been elusive so far.

In this dissertation I explore the age distribution of a population of adult lake sturgeon in a Canadian Shield river system for evidence of a density-dependent population bottleneck in the population's early life history by fitting an ARIMA autoregressive time series model. I find that there is an autoregressive relationship, whereby the presence of lake sturgeon from one to four years old is associated with lower recruitment of lake sturgeon into this juvenile stage. A slight improvement in recruitment is associated with five-year-old fish in the system. I infer that density negatively affects lake sturgeon in a short early-juvenile period. I describe characteristics of nursery areas that might partially account for this effect.

I then adapt a Lefkovich Matrix stock-recruitment model with density dependence expressed as a Ricker-modeled carrying capacity on year classes 0 to 5. The model is run with stochastic larval survival and vital rates specific to five life history stages of the lake sturgeon. In the model, simulated changes to juvenile carrying capacity drove recoveries and declines in the overall population within 25 years.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1: Introduction

The lake sturgeon (*Acipenser fulvescens*) is a large-bodied, slow growing member of the Acipenseridae family of Acipenseriformes, an order of Actinopterygii differentiated from the Teleostei by partially ossified cartilaginous skeletons, placoid scales, spiral-valve intestines, and a heterocercal tail (Pollock et al. 2014, Peterson et al. 2007). The Acipenseriformes are among the basal actinopterygians and resemble the teleosts in some key ways that differentiate them from the elasmobranchs and other cartilaginous fish (Warth et al. 2017, Gardiner et al. 2005). The sturgeon has an operculum, well-developed fin rays, and a swim bladder that is used to control buoyancy, although the swim bladder is physostomus and may be filled by gulping air (Logan-Chesney et al. 2017, Bruch et al. 2002).

The species is late maturing, with females in some populations not spawning until after 20 years of age. Males may begin spawning in their mid-teens (Peterson et al. 2007, Bruch et al. 2002). The species also reproduces slowly, with multiple non-spawning years intervening spawning events in females (Peterson et al. 2007, Craig et al. 2005). Rates of growth, maturation, gonadal development, and trophic position vary as physiological responses to the species' environment and may be affected by temperature, habitat quality, prey species, and density (Jacobs et al. 2017, Power and McKinley 1997, Fortin et al. 1995, Wang et al. 1985). Growth, behaviour and maturation rates may vary between nearby populations or even among individuals using separate habitat within the same system (Kessel et al. 2018, Barth and Anderson 2015, Haxton and Findlay 2008).

Adult, juvenile, and young-of-the-year lake sturgeon primarily eat benthic invertebrates, likely in a generalist manner (Barth et al. 2013, Jackson et al. 2002, Beamish et al. 1998). Adults may occupy a higher trophic position and be more piscivorous, even occasionally eating invasive species, such as round gobies (Jacobs et al. 2017). There is some evidence of cannibalism, particularly of eggs and larvae around spawning time (Barth et al. 2013, Jackson et al. 2002), although gape limitations may prevent cannibalism at larger sizes.

The lake sturgeon is present throughout central North America, with populations in the Mississippi, Great Lakes, and Hudson Bay watersheds. Although still fairly widespread, the species presents a conservation concern, with many populations reduced due to habitat degradation, habitat fragmentation, and historical overfishing (Bruch et al. 2016, Auer 1996b). Lake sturgeon are listed as threatened, endangered, or special concern in 19 of the 23 jurisdictions in the U.S. and Canada that comprise part of their original range. The species is listed as threatened province-wide in Ontario, and they are listed as threatened federally in Canada (Bruch et al. 2016). Commercial fishing for lake sturgeon has largely been closed, beginning with the U.S. waters of the Great Lakes in 1977 (Hay-Chmielewski and Whelan 1997), and continuing throughout the early 2000s. Recreational fisheries across the species' range have been closed or severely restricted for the past several decades, with Ontario's recreational lake sturgeon fishery being closed province-wide in 2007. In spite of efforts to protect the species from harvest, however, most populations recover slowly, and sometimes fail to increase at all (Haxton et al. 2014, Vélez-Espino and Koops 2009, Hay-Chmielewski and Whelan 1997).

Though the species' generalist strategy and robustness to wide-ranging environmental conditions as adults is notable, the lake sturgeon's partially migratory life history strategy (Kessel et al. 2018), seasonally and ontogenically varying home range size (Thayer et al. 2017, Barth et al. 2009), and distinct spawning habitat requirements together make them particularly sensitive to various kinds of habitat loss (Altenritter et al. 2013, Chiotti et al. 2008, Bruch and Binkowski 2002, Auer 1996a). Hydroelectric dams constructed in the late 19th to mid-20th centuries fragmented river-dwelling populations of the lake sturgeon, leading to declines and occasionally the extirpation of the species from reaches of certain rivers. Haxton et al. (2015) reviewed the situation for hydroelectric developments in Ontario. Many river and lake systems have also been impacted by agricultural runoff (Wolf River; Bruch 1999), industrial pollution (Rainy River; Merriman et al. 1991), mining (Seine River; Sowa 2002), accumulations of coal cinders from historical shipping (Huron-Michigan Corridor; Caswell et al. 2004), and coarse woody debris from log driving (Kenogami; Beamish et al. 1998). Some rivers within the species' range may also become unsuitable for lake sturgeon due to climate change (Lyons and Stewart 2014). With a goal to improve prediction of the outcome of conservation efforts, particularly those involving habitat, in this dissertation I will review the lake sturgeon's life history strategy and produce a model including important aspects of that life history.

The lake sturgeon is partially migratory, with some individuals residing in either lakes or rivers year-round, and some migrating from overwintering habitat in lakes to spawning and feeding habitat in rivers during the spring and summer (Kessel et al. 2018, Rusak and Mosindy 1997). Spawning habitat is generally located in the headwaters of rivers, below rapids, and in tributaries with depths between 1 and 5 m and substrates of cobble or gravel. Spawning typically occurs in areas with noticeable water flow that can be as fast as 1.5 m/s. Spawning is temperature sensitive and usually occurs between 13 and 18 degrees Celsius during a spring freshet. Incubation lasts between 5 and 10 days depending on temperature, with yolk-sac larvae settling into the substrate near the spawning site until the yolk is absorbed (Pollock et al. 2015, Bennion and Manny 2014, Boukaert et al. 2014, Dumont et al. 2011, Chiotti et al. 2008, Johnson et al. 2006, Caswell et al. 2004, Nichols et al. 2003, Bruch and Binkowski 2002, Auer 1996a).

Larval survival is very low, particularly prior to feeding, and mortality is very high throughout the first year (Caroffino et al. 2010, Pine et al. 2001). A spawning site tends to be spatially restricted, and a relatively high flow and combination of substrate and depth are often similar to the habitat found around hydroelectric facilities (Friday 2011, Auer 1996b). Eggs are sensitive to predation (Forsythe et al. 2013, Caroffino et al. 2011, Caroffino et al. 2010, Bruch and Binkowski 2002, Sulak and Clugston 1998), poor water quality (Duke et al. 1999), scouring from moving substrates during high flows prior to hatching (Forsythe et al. 2013), and dewatering prior to hatching (Friday 2011). The latter two effects can be exacerbated by changes to flow regimes with river management.

After absorbing their yolk sacs, lake sturgeon larvae drift downstream, eventually reaching juvenile or nursery habitat (Auer and Baker 2002). Juveniles use nursery habitat in a manner characterized most broadly by limited home range size for several years before moving into habitat use patterns that more closely resemble those of adults (Barth and Anderson 2015, Barth et al. 2013, Barth et al. 2011), often characterized by seasonal migrations out of river systems and into the shallow waters of lakes or reservoirs (Barth et al. 2011, Bruch and Binkowski 2002). Along with variation in the ontogeny of the species, the exact timing of this change in behaviours may be influenced by environmental conditions, growth rates, and local adaptation, and may vary among river systems. For the purposes of this dissertation I will consider the life history stage characterized by the year-round use of in-river nursery habitat to consist of juveniles, and the older stage that is not yet sexually mature but characterized by behavioural and habitat-use patterns similar to those of adults to be subadult fish. This simplification improves the comprehension of the models presented in this dissertation at the expense of some nuance in habitat use that may be structured in part by the size of individual fish.

Partial migration, dependence on the availability of spatially and temporally restricted spawning habitat, extended use of nursery habitat, and maturation into different habitat use and new behaviours prior to sexual maturation comprise a life history strategy that is not unique to lake sturgeon. As well as other acipenserids, many salmonids exhibit a similar strategy, including most anadromous salmon and char, coaster brook trout, and rainbow trout (Robillard et al. 2011, Jonsson and Jonsson 1993). Marine fish have been documented to have similar strategies, including Atlantic cod and Gulf menhaden (Jonsson and Jonsson 1993, Deegan 1993). This strategy is even present in many species of lamprey, including the sea lamprey, which often migrate to spawn in nursery beds that are subsequently and concurrently occupied by amocete larvae for multiple years (Beamish 1979).

Stage-structured populations and migratory or partially migratory life history strategies can complicate management efforts. Vital rates may vary between ontogenetic stages, and particular vital rates may vary among populations depending on environmental variables and local adaptations (Vélez-Espino and Koops 2009). Actions that change particular vital rates, such as closing fisheries to decrease adult mortality, may not impact other vital rates, such as fecundity or juvenile mortality (Vélez-Espino and Koops 2009, Jensen 1997). Similarly, other effects, such as density-dependent mortality or condition, may occur in only one life history stage due to spatial or temporal habitat segregation (Caswell and Takada 2004, Cooke and Leon 1976). My purpose in writing this dissertation is guided by the hypothesis that density-dependent effects limit some populations of lake sturgeon at a life history stage prior to maturity. My specific objectives are (1) to develop and test a method for detecting stage-structured density-dependent effects in a population of lake sturgeon using a mid-sized sampling effort conducted over a short duration, and (2) to describe a stage-structured, density-dependent effect in a mathematical model in order to predict the impact of density within a single life history stage for any population to which this description applies.

I will describe lake sturgeon in a stock-recruitment context with a particular focus on factors impacting the survival of the population prior to recruitment. The complex life history strategy of the lake sturgeon lends itself to describing recruitment as one of three separate events: (1) the settlement of larvae into nursery habitat at some point during the first year (Auer and Baker 2002); (2) the survival of juveniles to subadult stage where they begin to resemble adults in habitat use and behaviour, and likely catchability within a theoretical fishery; or (3) the survival of subadults to maturity (Peterson et al. 2007). For simplicity, unqualified uses of the term recruitment in this dissertation refer to recruitment from the subadult to the sexually mature adult stage, using an age cut-off appropriate to females. This assumption allows all recruits to have a theoretical fecundity, a feature important to most stock-recruitment models, and allows a size cut-off for recruitment close to the age that represented the highest point on catch curves for the study system, simplifying assumptions about the relative catchability of particular age and size classes.

Study Site

The Namakan Chain of Lakes (Figure 1.1) was chosen as a model system for this study. This chain of lakes is a series of Canadian Shield lakes and reservoirs that spans the Minnesota-Ontario border upriver of Rainy Lake. It includes six separate water bodies connected through narrow passages: Namakan, Kabetogama, Sand Point, Crane, Little Vermillion and Loon lakes. Water enters the chain of lakes through a number of rivers, including the Ash, Loon, and Namakan rivers (Shaw et al. 2012). Traditional ecological knowledge and direct observation suggest that some lake sturgeon spawning occurs in all three rivers, but the Namakan River's large size, long migratory corridor, notable presence of juvenile lake sturgeon, large number of spawning locations, and year-round occupation by adult lake sturgeon lead me to suspect that it is the largest contributor of fish to the system (Figure 1.2).

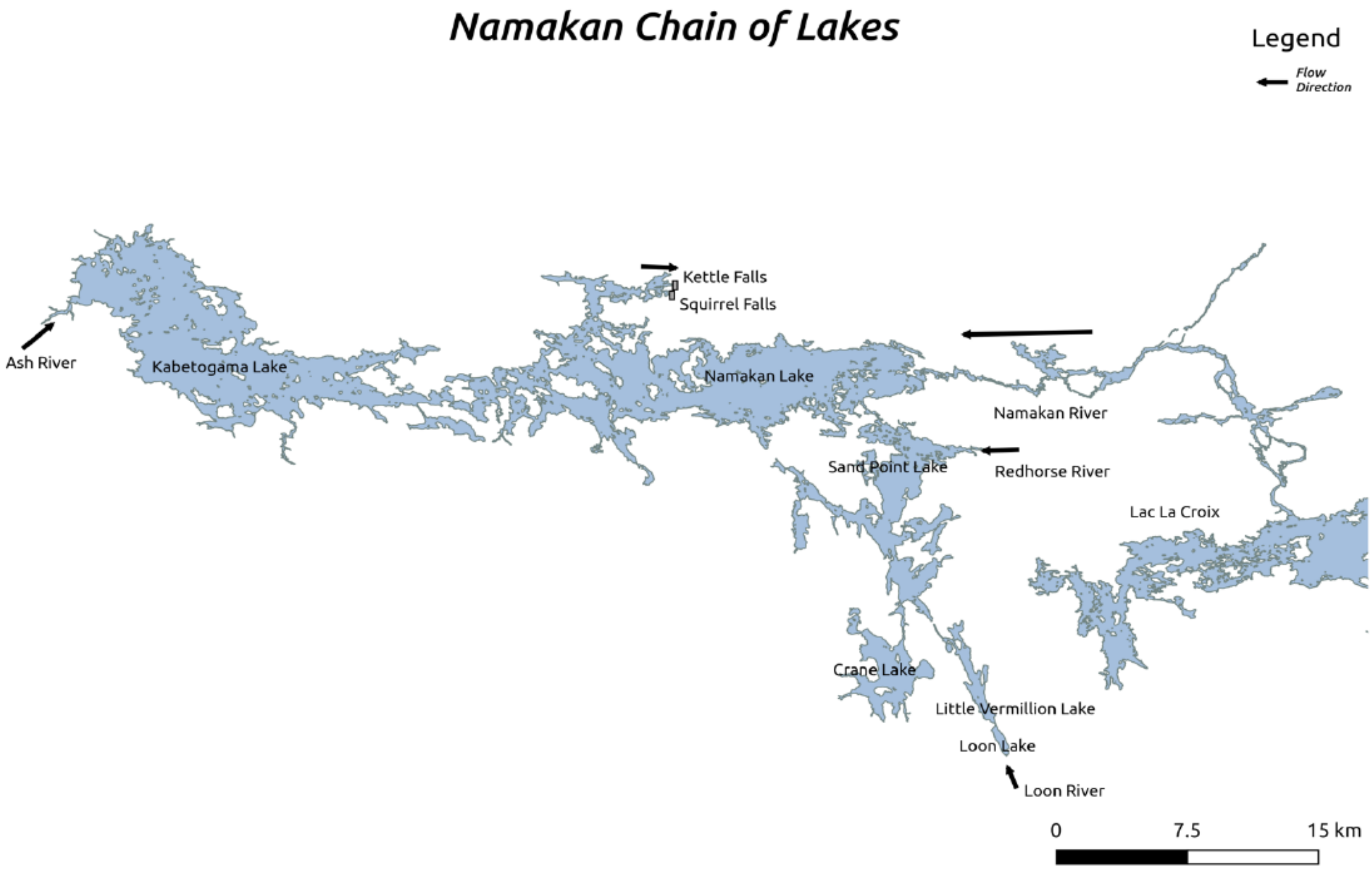


Figure 1.1: A map of the Namakan Chain of Lakes study area

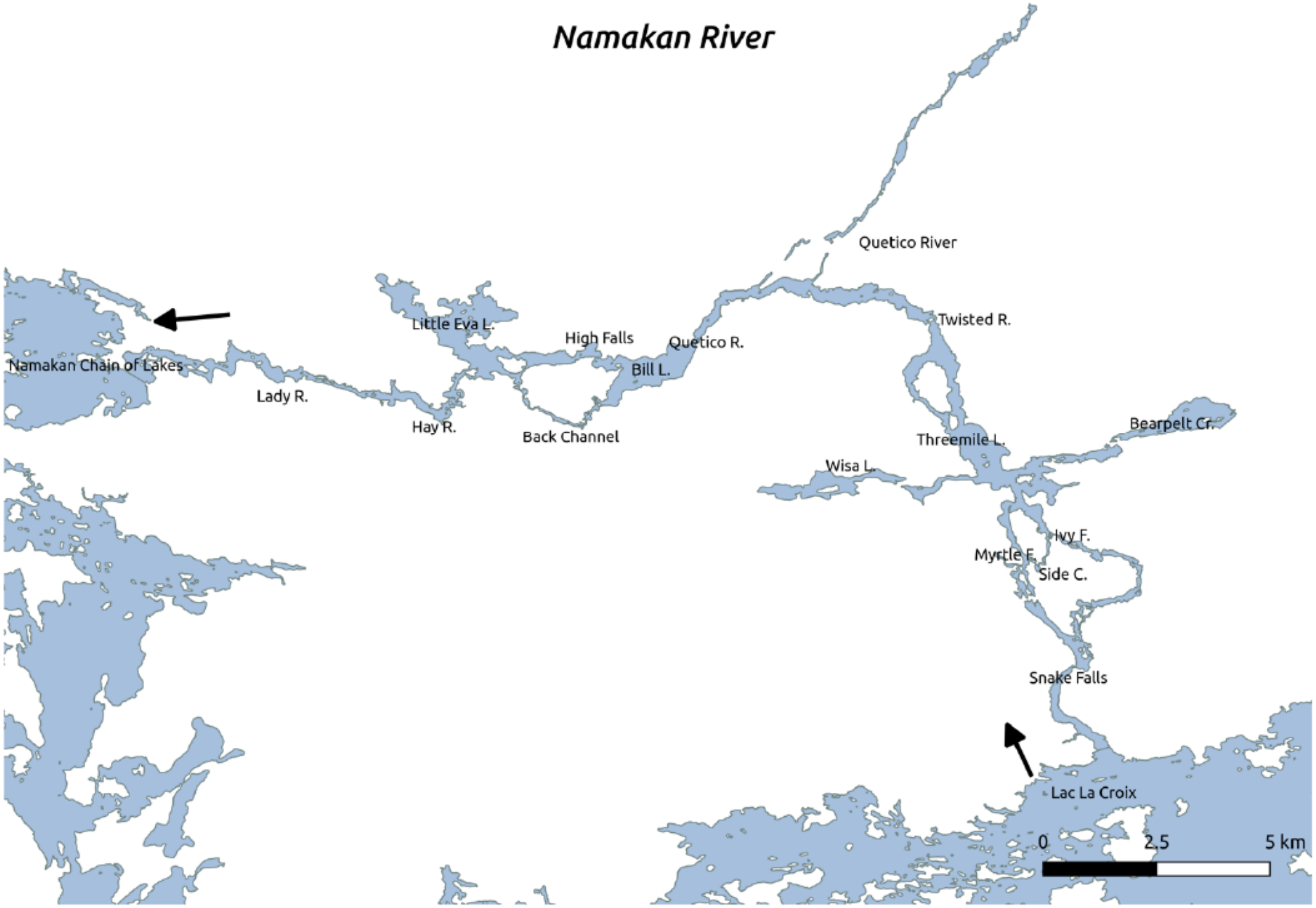


Figure 1.2: A detail map of the Namakan River study area

A pair of control structures located about 20 km downstream of the mouth of the Namakan River limits the outflow of water from Namakan Lake. The Kettle Falls and Squirrel Falls dams are used to control the height of water in the Namakan Chain of Lakes and improve the function of the International Falls Hydroelectric Generating Facility (Kallemeyn 1987). These two 4-m structures may modify the height and flow of water in the lowest reaches of the Namakan River and raise the height of water in the chain of lakes and may serve to restrict movement of lake sturgeon between the Namakan System and Rainy Lake.

The Namakan River (Figure 1.2) is a roughly 35 km stretch of river flowing from Lac La Croix (Minnesota and Ontario) to the Namakan Chain of Lakes (Minnesota and Ontario). The Namakan River is not located on the Minnesota-Ontario border, and is instead located entirely within Ontario. The river's roughly 30 m of gradient is lost in several large steps beginning at Snake Falls (river kilometre, rkm 30), dropping through Ivy Falls and Myrtle Falls and a connecting side channel at rkm 24, Twisted Rapids (rkm 19), Quetico Rapids (rkm 13), High Falls (rkm 10), Hay Rapids (rkm 8), and Lady Rapids (rkm 4; Shaw 2010). During a six-year-long study of acoustically tagged lake sturgeon in the Namakan River and Chain of Lakes no upstream movement of adult lake sturgeon past Snake Falls was observed, suggesting that Snake Falls is a natural barrier to migration (McLeod and Martin 2015, Welsh and Mcleod 2010). It is possible that Lake Sturgeon from the Lac La Croix/Maligne River population may occasionally emigrate to the Namakan River over Snake Falls. High Falls is circumvented by a small, seasonal side channel that is used during the spring migration to reach spawning sites in the upper river (McLeod and Martin 2015).

Three large, slow-moving parts of the main stem of the Namakan River are colloquially referred to as lakes. The most lentic of the three is Little Eva Lake, located between Hay Rapids and High Falls, which is a known overwintering location for river resident and two-step migratory adult lake sturgeon, where adults overwinter in the river for the year prior to spawning (McLeod and Martin 2015). Immediately above High Falls is Bill Lake, containing known nursery habitat for juvenile lake sturgeon (Trembath 2013). Above Twisted Rapids and below Ivy and Myrtle Falls is Threemile Lake. Three substantial tributaries flow into the Namakan River along its length. Wisa Lake joins Threemile Lake from the west over a beaver dam and an unnamed creek through a substantial stretch of wetland. Bearpelt Creek drains Wolseley Lake into the eastern end of Threemile Lake. The Quetico River joins the main stem of the Namakan River in two separate forks upstream of Hay Rapids, near rkm 15 (McLeod and Martin 2015).

Mean summer flows down the Namakan River range from about 100 to 400 m^3/s. A commercial fishery existed in Rainy Lake and the Namakan Chain of Lakes throughout much of the 20th Century, but the age structure of lake sturgeon in the Namakan Chain of Lakes does not appear to be biased toward younger fish. In fact, for year classes prior to 1983, annual mortality is estimated at a very low 4.8% (Shaw

2010). The catch curve appears to be smooth and resembles a log-linked Poisson distribution.

Habitat alteration within the Namakan River appears to include some influence below Lady Rapids of the Kettle Falls and Squirrel Falls dams (Kallemeyn 1987), some relatively unquantified modification of the main stem of the river for log driving, and some reaches of the river have coarse woody debris pollution from bark or sunken logs. Rock cribbing is evident at the top of High Falls, which may have been part of a log driving weir. A proposed hydroelectric development is planned at High Falls, but no construction has begun at the site.

Prior Work

The Namakan System's lake sturgeon population is reasonably well studied, having been the subject of multiple technical reports and two published papers prior to my involvement in the project. Work began as a collaborative effort between Voyageur's National Park, the Minnesota Department of Natural Resources, the Ontario Ministry of Natural Resources and Forestry, the USDA Forest Service, the 1865 Treaty Authority, and South Dakota State University (McLeod and Martin 2015, Shaw et al. 2012, Welsh and McLeod 2010).

Between 2004 and 2008, 533 lake sturgeon were captured and tagged by the multi-agency team in the Namakan Chain of Lakes, or by the Ontario Ministry of Natural

Resources and Forestry in the Namakan River (Shaw 2010). Of the captured lake sturgeon, 80 were implanted with Vemco (Nova Scotia, Canada) V16 acoustic telemetry tags and monitored by an array of Vemco V2R hydrophones placed throughout the river and chain of lakes (McLeod and Martin 2015). An additional 107 captures were conducted in the spring of 2012 and spring and fall of 2013, in order to better understand the population's reproductive structure. Lakehead University's Cameron Trembath (2013) captured 10 juvenile lake sturgeon in Bill Lake and implanted them with Vemco acoustic tags. An array of Vemco V2R receivers in Bill Lake was used to triangulate their locations during the summer of 2010, with 6 remaining to December 2012 within the array. Trembath characterized the depth and home range of juvenile lake sturgeon in Bill Lake, but he did not collect many habitat variables. The Namakan System is a good candidate for testing population models in a Canadian Shield river and lake system because it hosts a relatively healthy population of lake sturgeon with minimal modification, limited opportunities for migration into or out of the system, and a very even catch-curve distribution (Shaw 2010). CPUE for adult lake sturgeon in the Namakan River is high for adult fish and moderate for juveniles (Haxton et al. 2014).

Several attempts have been made to fit lake sturgeon populations into a stock-recruitment context to assess recovery potential and predict harm from specific activities. Perhaps notable among these models is Vélez-Espino and Koops's (2009) matrix model, which predicts that conservation of young adult lake sturgeon has the largest impact on fecundity and, consequently, population growth rate. Lake sturgeon populations have declined across their range, and consequently their adult populations are often assumed to be free of density-dependent effects, such as a population wide carrying capacity. The juvenile period, however, likely spans between 5 and 10 years, and is at least partially separated in habitat (Barth and Anderson 2015, Trembath 2013, Barth et al. 2013, Barth et al. 2011, Barth et al. 2009, Boase et al. 2008, Beamish et al. 1998). High larval production and steep early mortality curves could cause juvenile nursery habitat to reach very high population densities, even as adult populations recover.

In the following four chapters I will examine the Namakan River population in the context of early life history density dependence, testing the population for evidence that the hypothesized effect exists and building a stock recruitment model that builds on existing knowledge by including separate density effects at different life history stages. Two models will be used, an autoregressive model will be used in Chapter 2 to test for the presence of a stage-structured density-dependent effect and determine its magnitude if present, and a stage-structured Lefkovich Matrix Model will be used in Chapter 4 to calculate a theoretical population structure and simulate the effect of changing juvenile carrying capacities on the structure of the lake sturgeon population in the Namakan. Chapter 3 will provide a summary of some potential locations of juvenile nursery habitat in the Namakan River as well as a behavioural model to investigate habitat use.

Chapter 2: Recruitment out of the juvenile life history stage is density-dependent in lake sturgeon in a Canadian Shield river system

Introduction

Threatened and endangered fish stocks are typically below the carrying capacity of their environment (Pollock 2015, Vélez-Espino and Koops 2009). Lake sturgeon stocks are listed as threatened or endangered range-wide, and a number of conservation efforts are underway to either protect or bolster these populations, often with disparate methods (Pollock 2015, Thiem et al. 2013, Thiem et al. 2011, Haxton and Findlay 2008, Bruch 1999). Early and ongoing efforts include fisheries closures to protect existing stocks (Hay-Chmielewski and Whelan 1997), fish passage development to allow spawning adults access to historic migratory corridors (Thiem et al. 2011), trap and transport as an alternative to fish passage development (McDougal et al. 2013), spawning site restoration (Bouckaert et al. 2014, Dumont et al. 2011, Johnson et al. 2006), and artificial rearing (Crossman et al. 2009a, 2009b). In a species with a size structured, migratory or partially migratory life history strategy like the lake sturgeon, there may be separate, stage-specific density-dependent effects (Milner et al. 2003). Most models for recovering lake sturgeon stocks rely on the assumption that the entire population is below its particular river's carrying capacity. The related assumption is that the entire population is thus unaffected by density (Vélez-Espino and Koops 2009).

Building a better understanding of the life history strategy of the lake sturgeon is part of an ongoing effort to conserve the species (Wishingrad et al. 2014a, 2014b, Haxton and Findlay 2008, Nichols et al. 2003, Bruch 1999, Auer 1999, Sutton 1997, Chiasson et al. 1997, Auer 1996a). Much of the early effort focused on migration and the use of habitat by adult lake sturgeon, as well as describing and protecting spawning sites (Gerig et al. 2011, Friday 2011, Bruch and Binkowski 2002, Auer 1996a). In a traditional stock-recruitment context, these efforts should be among the most important in informing a conservation policy with the biggest impact as larval production and survival can often be increased by increasing available spawning habitat (Myers et al. 1995, Chadwick 1982). Lake sturgeon have long life spans, a protracted juvenile period, and, despite infrequent spawning through adulthood, high reproductive potential (Pollock et al. 2015, Boase et al. 2014, Barth et al. 2009, Vélez-Espino and Koops 2009, Auer and Baker 2002). However, even when impediments to population growth are not present, populations recover slowly (Haxton et al. 2014). Recent work with juvenile lake sturgeon, including that presented in this dissertation, describes year-round, in-river juvenile habitat as partially distinct from the habitat used by adults (Boase et al. 2014, Trembath 2013, Barth et al. 2011).

I hypothesize that lake sturgeon recruitment and thus population size are limited by a carrying capacity present in nursery habitat occupied by juveniles of the species. If present, this effect should be observable as a population-wide autocorrelation in year-class strengths, where the presence of strong year classes would predict subsequent weaker year classes in fish that were present in nursery habitat at the same time. The objective of this chapter is to apply an autocorrelative model to the age-structure of lake sturgeon in the Namakan Chain of Lakes to test whether a relationship consistent with early life history density dependence exists.

The Namakan River has undergone minimal anthropogenic habitat modification, but habitat degradation from log driving and the construction of two low-head control structures downstream of Namakan Lake in the early 20th century is suspected to have decreased the population from historic levels (Shaw 2010). The population of lake sturgeon in the Namakan System does not appear to be affected by density-dependent mortality at the adult stage, but age-related catch curves from earlier work in the system provide some evidence that the population is stable with fewer adults than the historical carrying capacity (Shaw 2010). This evidence includes a relatively even age distribution for adults, for which annual mortality was estimated at 4.8% (Shaw 2010), lower than the species average (Vélez-Espino and Koops 2009).

Contemporary harvest is restricted to a subsistence fishery, though commercial and recreational harvest were historically allowed in the system (Shaw 2010). Adult mortality additionally explains most of the inter-annual variation in year-class strength, with somewhat stronger year-classes related to lower average temperatures during the first fall of development and higher annual precipitation (Shaw et al. 2012, Shaw 2010).

Residuals from catch-curve analysis are non-cyclical and follow no obvious trend, indicating that variation is not directly relatable to the effect of greater spawning success from particularly strong parental year classes. Deviations from the mean function which appear to be random, are good candidates for fitting an autoregressive integrated moving average (ARIMA) function as a time-series approach to modelling (Box and Jenkins 1976). The Namakan River is a relatively small system, and it is assumed for the purposes of this chapter that the lake sturgeon population within the system's growth and maturation rates (Appendix C) were relatively constant within the time series.

Model development

A density-dependent effect in a population should resemble an autocorrelation in a time series. In a system classically limited by a carrying capacity, it would be expected that particularly strong year-classes are both preceded by and followed by comparatively weaker year-classes, and *vice versa*. Where density dependence is seen across an entire population, recruitment is autocorrelated to the total number of individuals in the population. In such populations, fitting a simple logistic model, such as the Ricker or Beverton-Holt model, to age data may reveal an effect of density and even allow estimation of carrying capacity. If the density effect occurs in an intermediate stage of a complex life history strategy, with size- or age-based stages spanning multiple years, a different approach is needed. In the case where an autocorrelation exists within a subset of a time series, an ARIMA model can be used to predict its effect.

The ARIMA model describes a time series where the value of the function is assumed to be a linear combination of its own past values and the past values of an error term (Box and Jenkins 1976). The data used must be a stationary time series, containing no systematic change in the mean and no periodic variation (Stergiou 1991, Box and Jenkins 1976). ARIMA models are often used to forecast future values of time series and have been used to successfully predict lobster recruitment (Boudreault et al. 1977), tuna stocks (Mendelssohn 1981), and jack mackerel stocks (Stergiou 1991). Part of the predictive power of these models is that the autocorrelations and moving averages contained within them are related to biological phenomena (Tsitsika et al. 2007, Boudreault et al. 1977).

The ARIMA model has the benefit of using autocorrelations to forecast the outcome of a time series as well as providing a method of limiting the effect to a specific time window (Box and Jenkins 1976). Assuming a stage-structured density-dependent factor exists, the autocorrelative component of the ARIMA model should be representative of its effect on the lake sturgeon’s population dynamics, consistent with this chapter’s hypothesis, assuming that a particular stage of the population investigated is near its carrying capacity. The lake sturgeon has a high reproductive potential, limited juvenile habitat, and high early mortality, potentially validating this assumption (Caroffino et al. 2010, Vélez-Espino and Koops 2009).

The general form of the ARIMA model from Box and Jenkins (1976) is ARIMA (n,1,m):

$$\widehat{Y_t} - Y_{t-1} + \Theta_1 e_t + \ldots + \Theta_m e_t = \mu + \Phi_1 (Y_t - Y_{t-1}) + \ldots + \Phi_n (Y_{t-n} - Y_{t-n-1}) \qquad (1)$$

where Θ_n are moving average (MA) coefficients related to change in the error term over time, and Φ_n are autoregressive (AR) coefficients related to the effect of previous values on the current value. The convention for labeling ARIMA models is ARIMA (n,l,m), where n is the number of autoregressive components, l is the order of the differencing used to achieve stationarity, and m is the number of moving average components.

Box and Jenkins (1976) provide a method of fitting ARIMA models to time series. This method involves selecting a stationary model, estimating the parameters, and checking the model to ensure that it conforms to a stationary univariate process. In this case, I will use my hypothesis of density dependence to guide selection of candidate models, use maximum likelihood estimation to generate the model parameters, and check the stationarity of each resultant model. I will then use information theoretical methods to determine which model is the most parsimonious.

Materials and Methods

Captures

Initial lake sturgeon captures in the Namakan Chain of Lakes were undertaken from 2004 to 2009 in a partnership between Voyageurs' National Park and the Ontario Ministry of Natural Resources and Forestry (Shaw et al. 2013). These captures occurred throughout the Namakan Chain of Lakes and the Namakan River with 150-, 200-, 250-, 300- and 350-mm stretch mesh gillnets. A pectoral fin ray clip was collected from each individual caught, and each was released back into the river system (Shaw et al. 2013). A total of 277 fish were captured as part of the joint effort to tag adult lake sturgeon and determine likely spawning sites within the system, with an additional 256 captured within the Namakan River by the Ontario Ministry of Natural Resources and Forestry in the spring and fall of 2006 and 2007. All 533 samples were pooled in this analysis. Summary information from these captures is included in Appendix D. Additional adult lake sturgeon were captured in the fall of 2013 using the same capture and collection methods.

Ageing

Pectoral fin rays were sent to the Ontario Ministry of Natural Resources and Forestry fish age facility in Dryden, Ontario for age analysis. Each fin ray was sectioned using a lapidary saw and mounted in epoxy resin on a slide for microscopic analysis. Annuli associated with seasonal growth were counted outward from the centre of the fin ray to the margin, counting the first translucent annulus as the end of the first year. The annular count was used to produce an estimate the age of each fish, along with an associated confidence. Fin rays without ages and with low ageing confidence were removed from the age distribution. The distribution of ages was used with no correction factor. It is, therefore, likely that the counts of annuli underestimated the true ages of the fish (Bruch et al. 2009), but they were likely accurate relative to each other. Errors associated with the subjective nature of interpreting fin rays were reduced by comparing ages from the same population assessed by the same person (Bruch et al. 2009, Rossiter et al. 1995).

Data analysis

The age dataset was cleaned by removing unreliable ages and ages lower than the mode of the catch curve, which were considered too small to be fully recruited to the gear (Maceina 2004). A length-class distribution was built from the resultant fish as a check on the assumptions of the model.

The ARIMA model assumes that the time series is stationary. The time series generated from fin ray sampling over a short period of catches represents a catch curve with trends associated with annual mortality and the size-selectivity of the gillnets used for sampling (Shaw 2010, Maceina 2004). The underlying trend is not stationary and the time series must be transformed into a stationary time series. Accordingly, I detrended the age distribution in the sample both using Poisson regression to a natural log linked catch-curve model to account for mortality only (Maceina 2004) and using the more general technique of first-order differencing (Stergiou 1991, Box and Jenkins 1976). I tested each of these detrending models for stationarity using the Dickey-Fuller Test (R Time Series Package). I then fit a number of candidate ARIMA time series models to the age data using the Time Series (c) package in R (Rmetrics Core Team, Setz et al. 2015, Box and Jenkins 1976).

Candidate models

If lake sturgeon undergo a stage-specific density-dependent effect limited to the juvenile stage, I would expect autoregressive and potentially moving average factors in their age distribution to closely follow the length of the juvenile stage. In this study population, the juvenile stage likely corresponds to between one and six years (Trembath 2013). Accordingly, candidate models were all ARIMA models with between zero and six autoregressive parameters and between zero and six moving averages. Six years was selected as the upper limit of possible ages for juvenile lake sturgeon in the Namakan River also because this year may correspond with ontogenic changes in habitat use.

Model selection

The candidate ARIMA models were selected by running the largest model first and then eliminating factors until every coefficient was significant. Every model less complex than the full model was compared, and those that did not meet stationarity criteria, where the absolute value of the coefficient of any factor was not significantly less than 1, were subsequently discarded. The remaining models were compared using the Akaike Information Criterion (AIC) to determine the best fit and most parsimonious.

Results

The 1981 cohort was the first determined to be fully recruited to the gear used in the 2004 to 2008 sampling. A total of 455 adult lake sturgeon of the initial sample of 533 were thus considered both fully recruited to the sampling gear and aged confidently enough to be used in the sample. Both particularly strong and weak year classes were detected in a non-cyclical age distribution. Age classes appeared to follow a similar distribution to length classes in this system (Figure 2.1). Captures and CPUE were distributed throughout the system and the relatively even catch curve adds some confidence that the sample is representative of the system (Figure 2.2). The mean weight at 1000 mm was 5.65 kg and the mean total length of 23- to 27-year-old individuals was 1185 mm, somewhat smaller and lower condition than the Rainy Lake and Lake of the Woods populations (Shaw 2010).

Of the three distributions tested (the raw age class distribution, the distribution of residuals around the catch-curve model, and the first-order differenced model), only the first-order differenced count data met the stationarity assumption of the ARIMA model. The age distribution of the raw sample fit a catch curve consistent with the

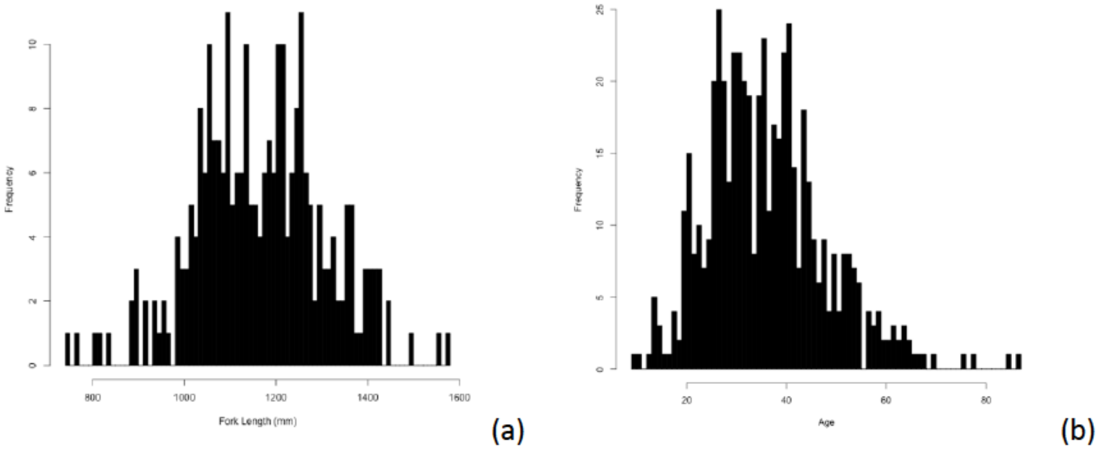


Figure 2.1: (a) Length-frequency distribution for all lake sturgeon captured in gillnet sampling targeting adult lake sturgeon in the Namakan Chain of Lakes from 2004 to 2008. (b) Age-frequency distribution for all lake sturgeon caught in gillnet sampling targeting adult lake sturgeon in the Namakan River and Chain of Lakes from 2004 to 2008. Condition data are in Appendix D.

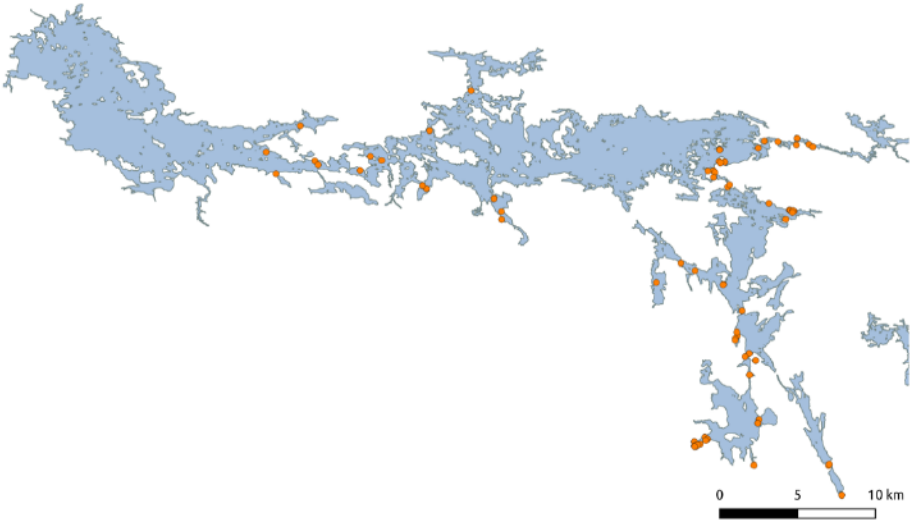


Figure 2.2: Capture locations (orange) of adult lake sturgeon sampled during spring and fall sampling in the Namakan Chain of Lakes from 2004 to 2008. Additional captures were made in Little Eva Lake and Bill Lake in the Namakan River (not pictured).

effect of mortality, violating stationarity assumptions. The residual age distributions from the best-fit catch curve also violated stationarity assumptions, perhaps owing to an additional trend that was not addressed in the catch-curve model from Maceina (2004). A comparison of the three corrected time series is presented in Figure 2.3. Consequently, I considered only first-order ARIMA models in this analysis. Input data were differenced ($Y = X_t - X_{t-1}$).

The most descriptive ARIMA model that included only significant factors was the first-order ARIMA model with five lagged autocorrelations and three lagged moving averages, although this model was not stationary. This model (ARIMA 5,1,3), along with ARIMA 2,1,1 were not considered because they did not significantly differ from models that violated stationarity (Table 2.1). Of the remaining models, ARIMA 5,1,0 had the lowest AIC score and was chosen as the best model. The relative success of any given age class in this model had a strong negative correlation with the relative recruitment success of the previous year’s recruits and recruits the year before that having autoregressive coefficients of -0.61 (95% CI: -0.48 to -0.76) and -0.63 (95% CI: -0.48 to -0.78) respectively. The recruitment of the age classes three and four years older also had a negative impact in this model with weaker negative coefficients of -.27 and -0.15 respectively. The age class five years prior was slightly correlated with a higher level of recruitment with a coefficient of 0.20 (95% CI: 0.07 to 0.33).

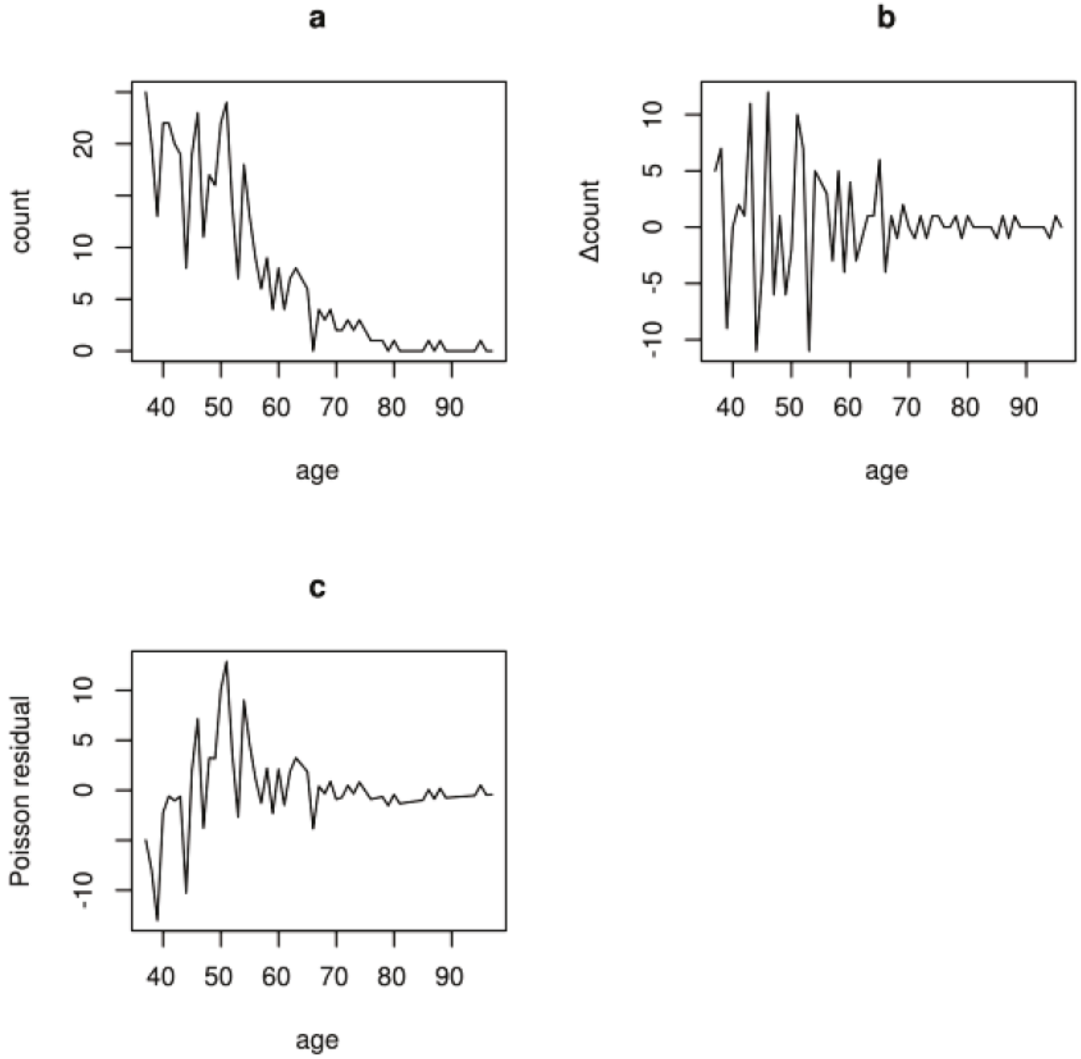


Figure 2.3: (a) The raw catch-curve of all lake sturgeon captured in the Namakan River and Chain of Lakes between 2004 and 2008 that were fully recruited to the gear. (b) The catch curve of all fully recruited adult lake sturgeon captured in the Namakan River and Chain of Lakes between 2004 and 2008 detrended by taking the first-order difference. (c) The catch-curve of all fully recruited lake sturgeon captured in the Namakan River and Chain of Lakes between 2004 and 2008 detrended to the residuals of a mortality-driven log-linked Poisson regression. Of the three curves, the only stationary distribution is generated by first-order differencing (b). Both the raw data (a) and Poisson residuals (c) have evident underlying trends that preclude their use in an ARIMA (n,0,m) model. Ages were computed from year-class in 2017.

Table 2.1: ARIMA coefficients for time-lagged autocorrelated models of recruitment success in the Namakan River $\boldsymbol{AR_n}$ *coefficients describe the autocorrelative relationship between the recruitment success of a given year-class and the year class n years older.* $\boldsymbol{MA_n}$ *coefficients describe the moving average change in variance between a given year and n years prior. The most descriptive model contains 5 autocorrelations and no moving averages. The first four AR coefficients are negative, suggesting reduced recruitment success as the result of the increased presence of year-classes one to four years older. The fifth AR coefficient is slightly positive, indicating improved recruitment success when fish five years older are present.*

Model	AR 1	AR 2	AR 3	AR 4	AR 5	MA 1	MA 2	MA 3	AIC	ΔAIC
5,1,0*	-0.61	-0.64	-0.27	-0.16	0.20	-	-	-	327.15	0.00
0,1,3*	-	-	-	-	-	-0.64	-0.18	0.35	327.41	0.26
4,1,0*	-0.66	-0.72	-0.41	-0.29	-	-	-	-	327.47	0.32
3,1,0*	-0.60	-0.57	-0.24	-	-	-	-	-	330.40	3.25
2,1,0*	-0.50	-0.45	-	-	-	-	-	-	331.74	4.59
1,1,0*	-0.33	-	-	-	-	-	-	-	342.40	15.25

When used to predict future recruitment, ARIMA 5,1,0 produces a damped oscillation. There is a tendency for the model to reduce its variation over time when used to predict the relative contribution of year classes younger than the 1981 cohort that was the youngest included in this study (Figure 2.4). Predicted recruitment indices oscillate around and eventually converge on a relative contribution of about 20.6 sturgeon per year class to a theoretical future sample, a value that is likely proportional to the system's carrying capacity for juvenile lake sturgeon.

Discussion

The ARIMA 5,1,0 model can be interpreted as the effect of a density-dependent factor acting on juvenile lake sturgeon in the study system. In this model the relative recruitment success of the four prior years was negatively autocorrelated with the recruitment success of a given year's age class. The five-year duration of the autocorrelative effect is much shorter than the approximately 50-year duration of the species' adulthood, and the population of adult lake sturgeon in the Namakan System is considered to be below its historical carrying capacity (Shaw 2013), lending support for the idea that the autocorrelative effect is contained within the shorter juvenile period. Because juveniles use habitat differently from adults in this system (Trembath 2013), the mechanism for this autocorrelation is most likely density-dependent mortality within nursery habitat.

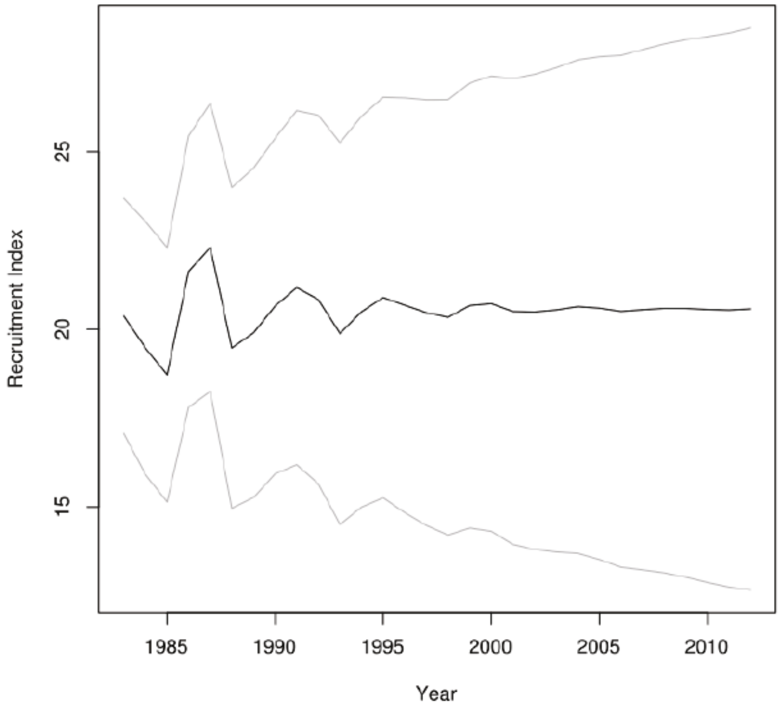


Figure 2.4: The predicted recruitment from year-classes younger than the first fully-recruited year-class in 2008 (1981) in a theoretical future sample taken under identical conditions. Grey lines highlight the 95% confidence interval. The value of the function without error produces a damped oscillation that converges on a constant contribution of 21 fish per year. Some level of stochastic variation is necessary to maintain continued oscillations in this model.

It is interesting that the recruitment success of any given age class correlates positively to the success of the group five years older. Six-year-old fish, which may occupy the same habitat as juveniles at younger ages and compete with these younger conspecifics (Boase et al. 2014, Altenritter et al. 2013, Barth et al. 2009, Chiasson et al. 1997), appear to positively impact the success of one-year-olds. This outcome might be an effect of errors associated with the subjective nature of interpreting fin rays, but since ages were all from the same population and assessed by the same person, it is likely that the ages are accurate relative to each other (Bruch et al. 2009, Rossiter et al. 1995). It is possible that the positive effect of older juveniles is due to the relatively stronger impact that those juveniles have already had on the intervening year classes (with AR coefficients of -0.61 and -0.63 on the two subsequent year classes), or that size-structured habitat use within the juvenile stage alters the density effects between years. The sixth year of life may also be a point in the ontogeny of lake sturgeon at which changes in habitat use or behaviour begin to differ substantially from the juvenile stage.

The potential exists for systematic underestimations of the ages of adult lake sturgeon, particularly in older animals (Bruch et al. 2009). This effect may be minimized by the relatively short five-year duration of the autocorrelative effect, but the loss of annuli in older fish at its extreme may contribute to an underestimation of the duration of the effect. The exact timing of the ontogenetic change contributing to the end of the effect should be confirmed by analysing a time series of lake sturgeon under 15 years of age, where inaccurate counts of annuli are minimised (Bruch et al. 2009).

Since variation in recruitment does not appear to be cyclical, it is unlikely that ARIMA autocorrelations are related to particularly strong year classes all spawning in the same years. The strength of spawning is highly variable in lake sturgeon, but if spawning and subsequent larval survival are strong enough to frequently bring juveniles to a level near their carrying capacity, the density-dependent factor illustrated here would likely be present. Lake sturgeon recruitment is variable within populations across the species' range and dependent on habitat, population health, and flow regulation (Haxton et al. 2015). Recruitment success associated with larval survival could drop as a result of environmental conditions during or after spawning (Haxton et al. 2015, Forsythe et al. 2013), predation (Waraniak et al. 2017, Forsythe et al. 2013), or lack of migratory access to spawning habitat, which may occasionally occur with low flow in the Namakan River (McLeod and Martin 2015). Recruitment out of the juvenile stage may vary for similar reasons.

Although even unregulated river systems have highly variable recruitment (Haxton et al. 2015), it is unlikely that particularly strong or weak age classes caused by environmental variation are responsible for the fit of the ARIMA model. Larval mortality caused by environmental variations or failed spawning years would likely cause large, single-year variations in a pre-recruitment population. Such variations unrelated to density or year-class strength would weaken the fit relative to the previous year, but the response to these unusual years would be detectable by the model. The model's ability to detect autocorrelations separate from random noise suggest that the autocorrelation observed is, in fact, a feature of the population. Given the model's tendency toward equilibrium at a juvenile carrying capacity under non-varying conditions, it is likely that some stochasticity in larval mortality or spawning success must be present in the study system in order for the model to fit. A low recruitment coefficient of determination, indicating high variability in recruitment success, could be partially explained by density dependence in combination with other factors.

Juvenile lake sturgeon habitat seems to be far more restrictive than the habitat used by the adults of the same species. Juveniles are often detected in deeper water in slow moving reaches on the boundaries between lotic and lentic environments, although some exceptions exist, particularly in shallow river systems (Boase et al. 2014, Altenritter et al. 2013, Trembath 2013, Barth et al. 2009, Chiasson et al. 1997). A description of the habitat that juvenile lake sturgeon occupy in the Namakan River appears in Chapter 3 of this dissertation. Juvenile lake sturgeon grow faster than adults do, and accordingly have high per-weight caloric demands (Pollock et al. 2015). A combination of restricted habitat and high growth rate likely contributes to a relatively more competitive landscape for juveniles than for adults. High densities of juveniles may also make them more susceptible to predation (Waraniak et al. 2017). This effect is seen in other fish species (Holbrook and Schmitt, Anderson 2001, Hixon and Carr 1997).

Auer's (1996a) association of larger migratory distances during spawning with the health of lake sturgeon populations may be explained by juvenile habitat availability if juvenile habitat is limited by shorter migratory distances. If recruitment is limited by limited nursery habitat in systems like the Namakan River, the same effect may also limit the success of certain types of conservation efforts. Stocking and spawning habitat improvements may not improve the speed of recovery and may amplify density-dependent mortality, while conservation efforts focused on improving the quality and availability of juvenile habitat could be expected to increase recruitment and speed up recovery.

If available habitat limits the survival of larval or juvenile lake sturgeon over the period of more than one year, recruitment for any age class should be diminished with respect to the recruitment of older age classes that were present in nursery habitat at the same time. Detecting this pattern depends on annual spawning and a defined number of years spent in nursery habitat, a relatively even age distribution for adult lake sturgeon, and low adult mortality. With an annual adult mortality of 4.8%, the Namakan System has lower mortality rate than the species average (Shaw 2010). Adult mortality additionally explains most of the inter-annual variation in year-class strength

($r^2 = 0.85$), with somewhat stronger year-classes related to high annual precipitation and lower average temperatures during the first fall of development (Shaw 2010).

The objective of this chapter was to determine whether an autocorrelation resembling a density-dependent effect is present in the age structure of lake sturgeon in the Namakan Chain of Lakes, and to determine the extent to which this autocorrelation is present. The significance to other lake sturgeon populations of this effect should be of interest in describing and protecting nursery habitat. The model output generated from this analysis also establishes the juvenile period that will be further considered in this dissertation as ranging from one to five years of age, representative of the entire duration during which recruitment of a year class negatively impacts recruitment of subsequent-year classes. This definition will be used in Chapter 4 to establish the transition point between the juvenile and subadult stages in a proposed stock-recruitment model for lake sturgeon.

Chapter 3: Habitat use by juvenile lake sturgeon estimated at two scales in a Canadian Shield river system

Introduction

The lake sturgeon (*Acipenser fulvescens*) is a long lived, large bodied acipenserid with a partially migratory life history strategy (Kessel et al. 2018, Rusak and Mosindy 1997, Auer 1996a). The species matures late, with females likely to spawn for the first time at over 20 years of age, and spawning occurs infrequently, perhaps every 4 to 9 years (Pollock et al. 2015, Peterson et al. 2007). The species also presents a conservation concern across its range (Bruch et al. 2016, Pollock et al. 2015, Vélez-Espino and Koops 2009, COSEWIC 2006), largely due to the effects of historical overfishing, habitat loss, and habitat degradation (Pollock et al. 2015, Peterson et al. 2007).

Lake sturgeon are large river specialists with adults overwintering in large lakes, estuaries, or the main stem of large river systems (Pollock et al. 2015, Peterson et al. 2007, Harkness and Dymond 1961). Populations of adults live throughout the Great Lakes, the Hudson Bay watershed, and the Mississippi River basin, often migrating from lentic overwintering habitat into rivers where they spawn and feed during the spring and summer (Bruch et al. 2016, Bruch and Binkowski 2002). Although not much research has been conducted on density dependence in adult lake sturgeon, it is unlikely that a carrying capacity for adults limits survival in such a species (Vélez-Espino and Koops 2009). A separate density effect could, however, can be part of the juvenile stage of the species, estimated at from one to five years old (Chapter 2), making identification of juvenile habitat of particular interest moving forward in conservation.

Juvenile lake sturgeon are often found in spawning rivers downstream of spawning sites. Juveniles appear to be river resident year-round in many systems (Boase et al. 2014, Barth et al. 2011, Haxton et al. 2011, Beamish et al. 1998, Chiasson et al. 1997), although they may also occupy parts of lakes and reservoirs (Hrenchuk et al. 2017, Altenritter et al. 2013, Smith and King 2005). It is unclear how much habitat is necessary to have a functioning juvenile nursery. Auer (1999) found that longer migratory corridors predicted healthier populations of lake sturgeon within the Great Lakes basin. This result may relate to some average amount of juvenile nursery habitat per kilometre of river for those systems.

The Namakan System has a very healthy population of lake sturgeon (Haxton et al. 2014) but a total migratory corridor, including both the rivers and the chain of lakes, of less than 100 km, far less than the roughly 200 km predicted by Auer (1996a) as required for healthy populations. It may thus be possible that the Namakan River has a high density of juvenile habitat or better-quality habitat than what might be typical of other river systems. The Namakan River contains the largest and most active spawning sites in the system, as well as the majority of lotic habitat accessible from the Namakan

Chain of Lakes. Earlier work by Trembath (2013) located juvenile lake sturgeon in Bill Lake and Little Eva Lake, two slow-moving reaches of the main stem of the Namakan River, confirming the presence of nurseries in the lower part of the river. Trembath (2013) did not sample upstream of Bill Lake (rkm 13), while similar habitat and some of the system's most active spawning sites are located between Bill Lake and Snake Falls (rkm 13 and 30).

The objectives of this chapter were to study the fine-scale movement of lake sturgeon within the known nursery habitat in Bill Lake and to confirm the presence of juvenile lake sturgeon nursery habitat in the Namakan River upstream of High Falls. This chapter relies on a combination of use-availability modeling based on a moving gill net survey and behavioural methods relying on acoustic telemetry, examining the movement of juvenile lake sturgeon through a nursery area. The goal of this study is to determine the extent to which the Namakan River is used by juvenile lake sturgeon.

Model development

Fine-scale location data generated using the Vemco VPS system (Vemco, Nova Scotia, Canada) suffers from two major flaws. The data from all telemetry systems are geospatially autocorrelated (Aarts et al. 2008, Patterson et al. 2008), and the sampling efficiency is collinear with habitat types, particularly with benthic animals where the substrate's acoustic properties can interfere with the propagation of an acoustic signal. Typical methods for dealing with the autocorrelation involve randomly subsampling locations, but the outcome still relies on the assumption that location points are evenly distributed in time, an assumption invalidated by non-random errors caused by sampling efficiency. One way to address both problems is to fit a Bayesian state-space model to the data (Patterson et al. 2008). The model used in this chapter is a Brownian random-walk model that describes differences in movement behaviour between substrates. The model consists of two equations: the observation model, which describes the distribution of locations that could have been detected by the array, and the process model, which describes an individual's movement through the system.

Vemco's VPS system provides two-dimensional locations based on a time difference of arrival calculation and uses the intersection points of hyperbolas calculated from each receiver (Espinosa et al. 2011). The errors generated follow the shape of the hyperbolas and are non-uniform in space, but I will consider the limiting case to be a Gaussian normal distribution centred on the detected location when measuring distances between locations. Vemco also provides horizontal position error (HPE), a unitless measure of precision, with each point. HPE is proportional to the actual measurement error, allowing an observation model:

$$X = x + e \qquad (1)$$

where X is the actual location, x is the detected location, and e is a Gaussian random variable proportional to HPE.

Movement behaviour can be approximated with a random-walk using a general Brownian random-walk model:

$$X = X_0 + d \ (2)$$

where X is the current location, X_0 is the previous location, and d is the distance moved between time points. Since the Bill Lake samples are not uniformly distributed in time, the movement distance can vary depending on the time interval between points. This makes the movement rate (distance/time) more informative than distance for the behavioural model. I can correct the process model for this difference by multiplying the movement rate by the time between samples:

$$X = X_o + r(t) * t + \beta \qquad (3)$$

where r is the movement rate and t is the time between samples β is the random variation between movement distances.

Movement rates are unlikely to be constant between samples, so I adjusted them with a Gaussian random variable to account for natural variation to produce the process model. Each individual's path was thus determined by calculating the two-dimensional Cartesian distance between each subsequent point, and the movement rate was determined by dividing this distance by the time between detections. Path data were split into separate datasets by substrate and individual and analyzed by fitting a random walk state space model as described in Patterson et al. (2008).

$$X = X_o + (r(t) + \beta) * t \qquad (4)$$

where β is a Gaussian random variable accounting for variation in movement rate. R + β is the desired information for comparison between substrate types. This model is hierarchical and fully Bayesian and was fit with an uninformative uniform prior, due to the variability in juvenile habitat use reported for lake sturgeon.

The model was fit to the Vemco data by sampling from the posterior distribution with Markov Chain Monte Carlo sampling in the MCMCpack R package. Twelve thousand samples were generated with the first 2,000 discarded as a burn-in period. The remaining 10,000 samples were thinned by a factor of 10 to reduce autocorrelations. The distribution estimates of the movement rates for each pairing of individual and substrate were calculated as a median and 95% credible interval for comparison.

Methods

Fish sampling

Gill net surveys were conducted during the summers of 2014 and 2015 on the reaches upstream of High Falls and downstream of Ivy and Myrtle Falls (Figure 1.1). All surveys were conducted using 50 m of 115 mm stretch-mesh monofilament gill nets set at depths between 10 metres and 15 metres. Nets were set perpendicular to flow in each location. Fish were captured and handled according to Lakehead University Animal Use Protocol 20-2011 and in accordance with the terms of an Ontario Ministry of

Natural Resources and Forestry scientific collector's licence and Endangered Species Act permit. Trembath (2013) surgically implanted acoustic tags in only juvenile lake sturgeon under 610 mm in fork length in his study, capturing only lake sturgeon under 12 years old according to the Von Bertalanffy growth curve for this system (Shaw 2010, Appendix C). This cut-off matches the extent of the early juvenile stage in Vélez-Espino and Koops (2009). In the gillnet survey used here, I only counted juvenile lake sturgeon up to a fork length of 630 mm, corresponding to the upper bound of the length at twelve years of age in the von Bertalanffy growth equation (Appendix C). Twelve years likely includes both juvenile and subadult fish, depending on the exact timing of this change, but this capture range allows for a conservative estimate of habitat use, especially in light of the rapid and variable growth typical of this age-range.

Habitat survey

Depth and substrate surveys were conducted using a Humminbird 698 CI HD side-imaging SONAR system (Humminbird, USA) with a transom-mounted transducer. Substrate surveys were conducted using side imaging transducers in a single downstream transect along the thalweg of the river with a 100-m beam width. In wider areas of the river, supplemental surveys were conducted along transects perpendicular to the contour lines, in order to generate a more complete picture, as well as to eliminate distortions caused by the flat bottom assumption. Depth surveys were conducted in an upstream zig-zag pattern with the transducer configured to record depth and location at 10 Hz. Substrate data were collected with a modified version of Kaeser and Litts's (2010) method for habitat surveying with low-cost side-scanning SONAR systems.

Side scan transects were conducted perpendicular to the known depth contours of the lake in order to minimize distortions caused by the side-scanning system's flat-bottom assumption (Tessier 2015). SONAR and GPS tracks were exported from the unit and converted to comma-separated variables using GPSBabel (Robert Lipe, USA). Contour lines were interpolated in QGIS (Open Source Geospatial Foundation 2009) using the contour plugin and the points thinned by a factor of 100. Depth contours were overlaid on the Ministry of Natural Resources and Forestry's Ontario Base Map (OBM) water polygon layer to generate a depth map of the river. Side-scan data were radiometrically corrected and mosaicked into a raster image of the bottom using MB-System (MBARI, Moss Landing, California) and visually interpreted in QGIS. New depth soundings were used to re-interpolate the earlier depth map. This method for generating substrate maps was validated against information gathered using a submersible camera attached to an epibenthic sled by Tessier (2015).

The downstream distance of a sampling location from spawning sites was measured as the distance along the centre of the river between the nearest confirmed spawning site and the sampling location in QGIS using the OBM water layer. In order to determine the amount of available river habitat available at each sampling location, circles with diameters of one kilometre were generated in QGIS, centred on each sampling location. These circles were intersected with the map of the river, and areas of the resultant polygons were calculated.

Statistical analysis

Capture-no capture data were related to habitat variables using logistic regression in R. The tested habitat variables were depth, substrate, downstream distance from a spawning site, and area of river surrounding the sampling location. Selection of an appropriate logistic regression occurred by removing the least significant parameter from each previous analysis until a total of four equations were tested. The models were subsequently compared for parsimony using AIC. The model with the lowest overall AIC was considered the most parsimonious and, thus, most likely to be correct. Both probit and logit models were tested to verify that their results were the same.

State-space model

In 2010, 18 juvenile lake sturgeon between five and six years of age were captured in Bill Lake, a slow moving reach of the Namakan River near rkm 11 (Cameron Trembath 2013). Capture surveys used 30-m multifilament gillnets with panels of 76-, 102-, 128-, and 162-mm stretch mesh. Each of the captured fish was anesthetized in tricaine mesylate (TMS) and surgically implanted with Vemco V13 acoustic tags (Vemco, Nova Scotia, Canada) following Lakehead University Animal Use Protocol 19-2010 and a modified procedure outlined by Adams et al. (2006). Tags were configured for a nominal two-minute ping interval, where a ping was generated on a random interval between 90 and 150 s. The expected lifetime for the tags was two years.

Continuous monitoring occurred in an array of 6 Vemco V2R receivers. Each receiver consisted of a datalogger and hydrophone deployed one metre from the bottom tied to a subsurface float. The hydrophones were deployed in a ring around the deepest part of the lake, in order to maximize the spatial resolution of a Vemco VPS survey. Two stationary sync tags were placed in the centre of the array and used to synchronize the clocks on each of the devices. Each receiver's location and the location of the sync tags were measured from the surface with a Trimble sub-metre precision GPS device. Data collected by the receivers were downloaded in the fall of 2010 and spring of 2011 and were sent to Vemco for triangulation.

A grid of 30-m hexagons was overlaid on the study area with QGIS, and each hexagon was classified visually into one of three substrate types: rocks, gravel, or sand, by the prevailing substrate within the hexagon on the SONAR raster images. The 30-m resolution was chosen to match the maximum allowable error in the acoustic telemetry system. In cases where more than one substrate type were observed in a hexagon, the substrate that comprised more than half of the hexagon was identified as the primary substrate in that hexagon. There were no cases where any hexagon was not at least 50% covered with one substrate type.

The point files from Vemco's VPS analysis were filtered to remove detections of individuals that spent the majority of their time outside of the array, detections with a horizontal positioning error (HPE, unitless) of 30 or more, and detections that did not have a previous or subsequent detection within 30 min (Hrenchuk et al. 2017). The average interval between pings differed significantly from the two-minute nominal ping interval, and both the average ping interval and the variance differed significantly between substrate types, precluding the use of individual pings as an indicator of proportional time use.

Results

Capture locations

Juvenile lake sturgeon were captured at the confluence of the Quetico River, in Threemile Lake, and immediately upstream of Threemile Lake in 2014. In 2015, juvenile lake sturgeon were captured only in Bill Lake and at the confluence of the Quetico River. No juvenile lake sturgeon were captured in any of the narrower reaches between Bill and Threemile Lake except the mouth of the Quetico River (Figure 3.1). Juvenile lake sturgeon were caught in discrete areas at all distances downstream from the spawning sites and on all substrates (Table 3.1). These areas appeared to be generally wider reaches of the river (Figure 3.1).

Table 3.1: Juvenile lake sturgeon capture locations categorized by distance to the nearest known spawning site, nearby river surface area, depth, and substrate.

Spawn Distance (m)	Net Sets	Total Soak Time (hr)	Juveniles Captured	Depth (m)	Area (m)	Substrate
8761	2	23	1	12	374	Sand
7654	2	22	0	11	299	Rocks
6604	2	22	0	11	282	Rocks
5370	1	8	0	10	184	Rocks
4696	2	21	0	11	375	Sand
2596	2	22	1	13	672	Sand
2776	2	23	2	13	710	Sand
1522	2	23	2	16	174	Sand
302	2	23	0	16	302	Rocks
2801	1	18	2	11	381	Sand
1988	1	19	0	11	175	Sand
1483	1	19	0	11	239	Rocks
1216	1	20	0	10	241	Rocks
524	1	20	0	10	256	Sand
8923	1	20	1	10	279	Rocks

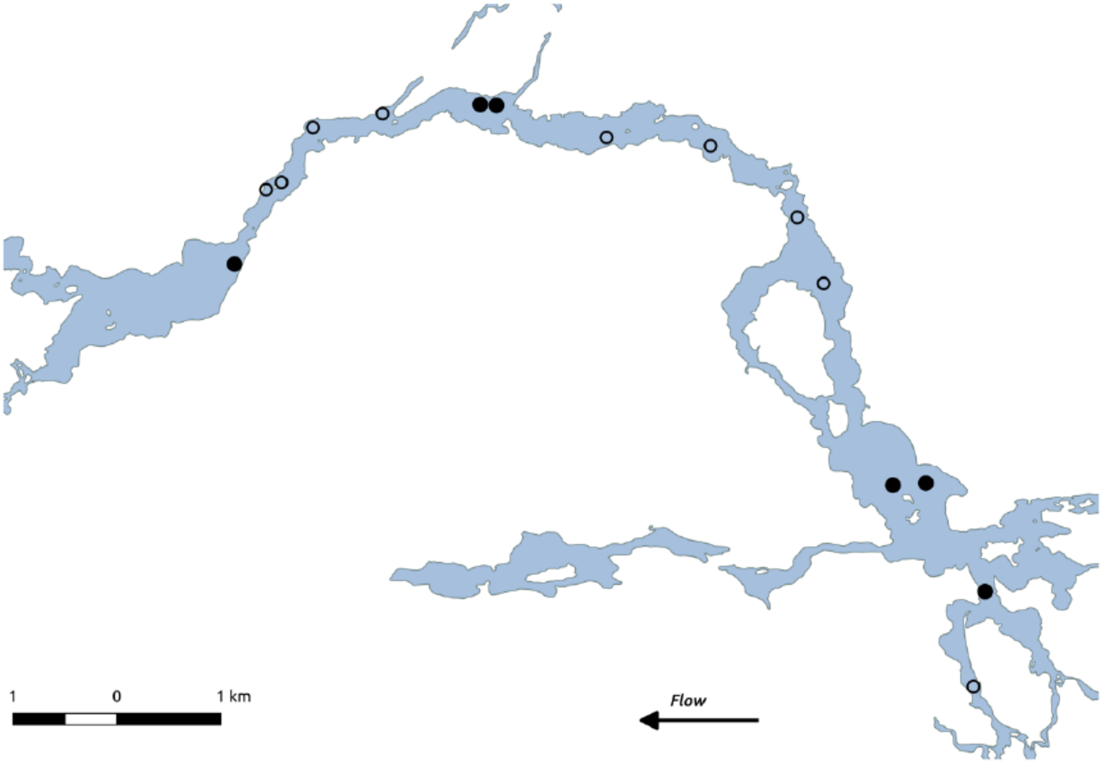


Figure 3.1: Juvenile lake sturgeon net sets and capture locations in the upper Namakan River. Circles indicate net sets. Hollow circles indicate locations where no juvenile lake sturgeon were found. Solid circles indicate locations where juvenile lake sturgeon were caught.

Habitat variables

Candidate logistic regression models containing all four variables (depth, substrate, distance from spawning sites, and surface water area) were significant, with small changes in AIC between each model. The parsimonious model contained only the area of water surrounding the sample location as a parameter (Table 3.2). The area of water surrounding the netting site was also the only parameter with a significant impact on capture in any of the models. In the best model, this parameter was significantly positively correlated with the probability of capturing a juvenile lake sturgeon at the site (P = 0.04, Log Likelihood = -5.53).

Table 3.2: AIC table for the four explanatory models for coarse-scale habitat use. The explanatory variables used were the depth, substrate type, distance in kilometres from the spawning site (DFS), and the total available habitat area. The best model included only habitat area.

	K	Log Likelihood	AIC	ΔAIC	AIC Weight
Area	2	-5.53	16.06	0.00	0.75
Substrate + Area	3	-5.32	18.81	2.75	0.19
Substrate + DFS + Area	4	-4.67	21.35	5.29	0.05
Depth + Substrate + DFS + Area	5	-4.41	25.48	9.42	0.01

State-space model

A mix of habitat types was detected within the Bill Lake survey area using the side-scanning sonar equipment (Figure 3.2). Substrate tended to be harder in the upstream portion of the survey area, with fine and very fine substrates in the downstream reaches. Five juvenile sturgeon were found to spend the majority of their time within the survey area. Although rates varied among both individual and substrate type, movement was generally slowest over rock substrates and fastest over sand (Figure 3.3). In all cases, the 95% credible intervals for each substrate-specific movement rate did not overlap.

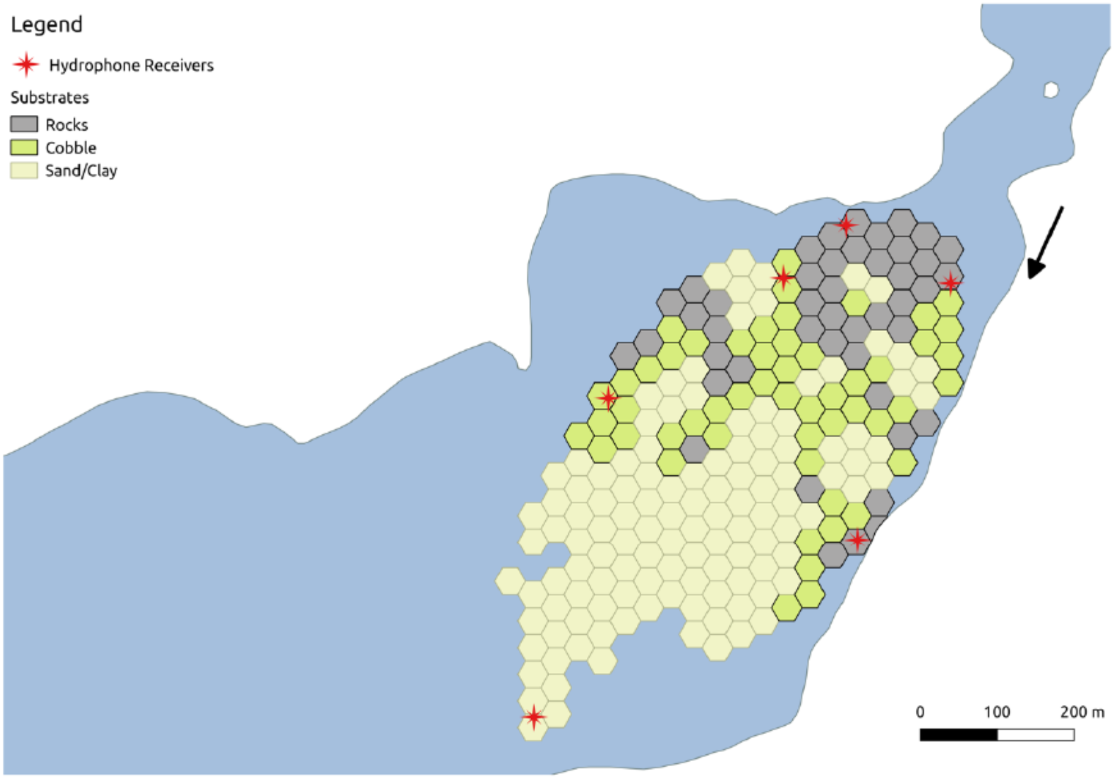


Figure 3.2: Substrate type in Bill Lake expressed as discrete hexagons. Harder substrates were found in the upstream areas in the North East. Very fine substrates were found in the downstream portion of the study area to the South West. Substrate was classified in this manner only within the area bounded by the telemetry hydrophone receiver array indicated in red. The most precise locations from the telemetry receiver array are within the area bounded by the receivers.

Three individuals (a, b & c) had matching movement rates over both rocks and sand, but they varied significantly over gravel and cobble. Two individuals (d and e) both had higher movement rates on average and did not show matching patterns for any substrate type. Four of five individuals moved slowest over rock substrates. Three

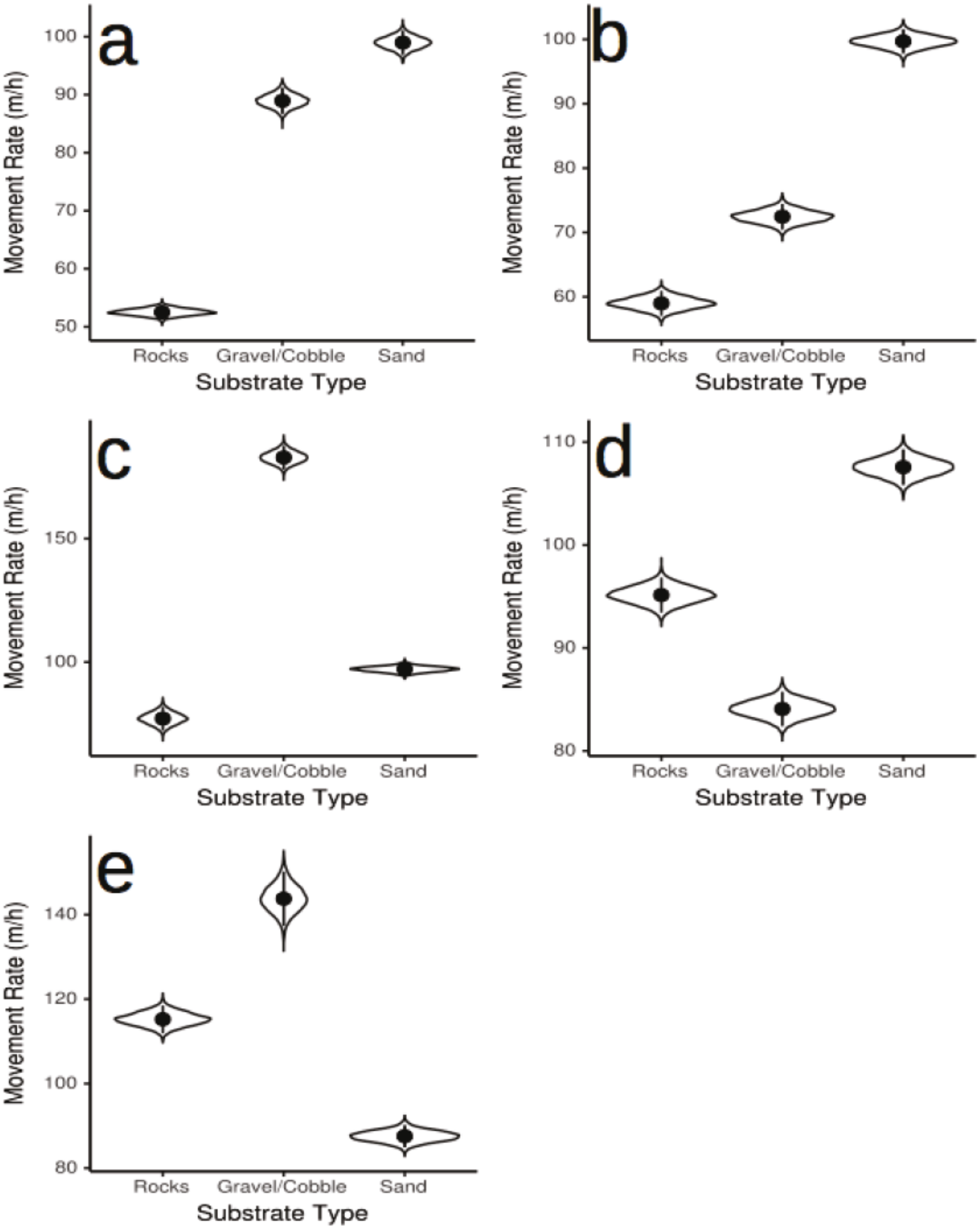


Figure 3.3: Violin plots of the modeled substrate-specific movement rates for the five juvenile fish that remained in the detectable area (a, b, c, d & e). Central points indicate median movement rates with bars

representing the 95% Bayesian credible interval for each value. Violin widths represent the probability density at each movement rate. Three of the five fish (a, b & c) moved slowest over rock substrates. Two (d & e) appeared to have alternate strategies.

of five fish moved fastest over sand. Movement rates over gravel and cobble were the most variable among the fish tested and did not match for any of the five fish. The particular ranking of each substrate's movement rate may indicate multiple habitat use strategies.

Discussion

Gillnet survey

The sample size of juveniles caught in the gillnet survey was very small, only nine individuals during two surveys. The best model to predict locations of juvenile lake sturgeon did not include depth, in contrast to other studies, but may be an effect of the small sample size and narrow depth range sampled in the Namakan System. Other studies focusing on depth of capture often located juveniles in shallower than the shallowest depths sampled in this study (8-25 m) (Barth and Anderson 2015, Altenritter et al. 2013, Barth et al. 2009).

If settlement were affected only by location at the end of a period of passive larval drift, nursery habitat would likely be found at distances from spawning sites consistent with the duration of drift, with no obvious habitat preference. The larval drift period is mentioned in the literature as an important part of juvenile habitat selection (Barth et al. 2009, Auer and Baker 2002), but in this study, distance from the spawning site was not related to the presence of juveniles, although all captures were downstream of known spawning sites, consistent with the findings of Boase et al. (2014). Findings here and elsewhere that the distance from known spawning sites does not likely affect the location of juvenile nursery habitat may indicate that settlement into nursery habitat is not passive and mediated by some level of habitat choice (Barth and Anderson 2015, Boase et al. 2014).

The area of water within one-half kilometre of the net location was significantly linked to the presence of juvenile lake sturgeon. The correlation was positive, predicting that sampling sites in wider reaches of the river, such as Threemile and Bill lakes, and in areas where multiple channels are available, such as the upstream end of Threemile Lake, the Quetico River mouth, and the confluence of Ivy Falls, Myrtle Falls and the Ivy-Myrtle side channel, were more likely to have a higher density of juveniles. This finding may be related to the need for a large amount of foraging area at this life history stage (Appendix B) or to the availability of specific physical habitat characteristics. The surface area of a reach may correlate negatively with water velocity, but juvenile lake sturgeon in this system occupy faster flowing areas of Bill Lake and may occupy sites with larger surface areas and faster moving water in this system (Trembath 2013).

The model linking the area of water within one-half kilometre of the net location to the presence of juvenile lake sturgeon conforms to the locations where juvenile lake sturgeon were captured by Trembath (2013): Bill Lake, Little Eva Lake, and the mouth of the Namakan River at Namakan Lake. The suggestion is that Threemile Lake, the Quetico River confluence, Bill Lake, Little Eva Lake, and the large, slow moving reaches near the Namakan River mouth provide the most important nursery habitat for lake sturgeon. Some additional areas predicted by the model that remain unconfirmed by my catch efforts are the downstream areas of Threemile Lake just upstream of Twisted Rapids, upstream of Quetico Rapids, and between Lady Rapids and Hay Rapids.

Juvenile lake sturgeon appear to occupy separate habitat from adults in this system as well as the closely associated Rainy Lake system. Adults appear to favour shallow habitat in lentic systems (McLeod and Martin 2015, Adams 2004). Juveniles, by contrast, seem to spend a great deal of time in the main channel of the spawning river, and can be caught at depths greater than 10 m. Given the relatively smaller home ranges of juveniles (Barth et al. 2009) and the migratory patterns of adults in this system (McLeod and Martin 2015), it is likely that juvenile nursery habitat is at least partially separated from habitat preferred by adults.

Since the identification and preservation of juvenile nursery habitat is a conservation priority (Pollock et al. 2015, Vélez-Espino and Koops 2009), and juvenile habitat as a likely bottleneck to recovery in otherwise well-managed systems (Chapter 2 of this dissertation), the identification of juvenile habitat is an important step in increasing lake sturgeon recovery potential. Additional juvenile lake sturgeon captures in areas identified here as candidate nurseries in the Namakan River could provide the density information necessary to identify measures of habitat quality, availability, and use in this system.

State-space model

Movement rates may be a reliable means of detecting behaviours associated with particular kinds of habitat use. Slow movements may be associated with foraging, as foraging animals may occupy particular foraging areas, frequently changing direction or stopping to consume prey. Slow movements may also accompany resting behaviours or be present in areas with lower predation risk. High movement rates, conversely, could be associated with cruising or movement between foraging patches. Although the sample size in this study was small and movement rates varied among the five continuously detected fish, this study may provide a framework for further investigation of data produced by an increasing number of acoustic telemetry systems. Juvenile lake sturgeon in this study appeared to have variable habitat preferences inferred from movement rates, with most seeming to prefer either rock or sand substrates, and highly variable use of cobble and gravel substrate types.

Since movement rates are calculated from two dimensional locations, vertical movements are not recorded, potentially biasing results toward lower movement rates if fish are traveling along the benthos in steep areas. This potential source of error may be minor given that juvenile lake sturgeon are not thought to use such high-slope areas (Chiasson et al. 1997), but diel movements and seasonal use of high slope areas may be missed with this method. Variability in sampling efficiency may also bias results by causing the calculation of slower movement rates in areas where sampling efficiency is low and fish are frequently changing directions, as may happen when foraging. This effect potentially exaggerates the reduction of movement rates in important foraging habitat when sampling efficiency is low.

Juvenile lake sturgeon have a noted preference for sand and softer substrates (Holtgren and Auer 2004, Chiasson et al. 1997). Substrate-specific movement rates that I measured were highly variable across individuals and did not demonstrate a preference for sand substrates. The slowest movement rates were detected in this study over both sand and rock substrates, and intermediate sized gravel and cobble substrates hosted a wider variety of movement rates. Thus, behavioural state-space modeling of movement rates in this system reveals an aspect of habitat use that may offer some important new insight into juvenile lake sturgeon ecology.

Chapter 4: Recovery potential of lake sturgeon in rivers with limited nursery habitat

Introduction

Estimates of recovery and recovery potential are the tool by which plans for conservation and harm minimization are evaluated (Pollock et al. 2014, Vélez-Espino and Koops 2009, Peterson et al. 2007). Determining recovery potential requires a mathematical model. Several stock-recruitment models are used for evaluating other stocks of fish but settling on one is difficult for acipenserids in general and for the lake sturgeon (*Acipenser fulvescens*) in particular. Simple logistic population growth, exponential models, and the Beverton-Holt model require too much precise data to easily fit to a population of animals with a high reproductive rate and variable larval survival like the lake sturgeon (Vélez-Espino and Koops 2009). The Ricker model gives a safer approximation of population growth in many fish species because it does not predict negative population growth where larval production is high (Ricker 1954). The direct application of the Ricker model, however, is frustrated by the species' late maturation, long lifespan, and age dependent fecundity. Chapter 2 of this dissertation provided evidence that a density-dependent reduction in recruitment may affect juvenile lake sturgeon in a river system like the Namakan. These features do not necessarily preclude the use of the Ricker model, but suggest that a more detailed model may produce better results.

Vélez-Espino and Koops (2009) proposed a stage-structured matrix model to evaluate allowable harm and recovery based on the structure and fecundity of lake sturgeon populations. This model has the distinct advantages of predicting specific outcomes based on harm or recovery efforts focused on specific stages of the lake sturgeon's life history, as well as being fairly robust to deficiencies in survey data in specific rivers. The exponential growth aspect of this model also allows fairly straightforward analytical evaluation of specific changes to various stage-specific vital rates through elasticity analysis. The results of these analyses are immediately valid but may lose their predictive capability over long time scales, particularly if a density effect is present in the population.

Habitat loss along with overfishing is one of the major causes of early 20th century population declines in lake sturgeon, with loss of access to spawning habitat a major source of concern (Pollock et al. 2015). Auer (1996a) notes that lake sturgeon require long migratory corridors to maintain viable populations in the Great Lakes. Rivers with impoundments for hydroelectric generation notably suffer both declines in abundance and have higher variability in recruitment than unmodified systems (Haxton et al. 2015). River systems are notable in lake sturgeon life history as areas with spawning sites and nursery habitats (Peterson et al. 2007). A lack of available nursery habitat could alter the carrying capacity for juveniles, as hypothesized in Chapter 2. The declines noted in Auer's (1996a) study, combined with the high and highly variable larval mortality observed in lake sturgeon generally (Caroffino et al. 2010, Vélez-Espino and Koops 2009), may be evidence that population size is at least partially limited by available nursery habitat.

Vélez-Espino and Koops (2009) note the importance of determining the extent to which density impacts recruitment in this species before directly applying their model to the data. In Chapter 2 of this dissertation, I presented an ARIMA model that shows the population structure of lake sturgeon in the Namakan River consistent with a population limited by density in its juvenile life history stage from one to five years. In this chapter, I will build an alternate form of Vélez-Espino and Koops's (2009) model to include a density effect of the abundance of one to five-year old juveniles on the survival of age-0 lake sturgeon. This life history stage may be the most susceptible to compensatory mortality from increased predation in less-than-ideal habitat or when individuals are confronted with competition for food (Ricker 1954). The stage is also known to experience highly variable mortality from year to year (Dumont et al. 2011).

The objective of this chapter is to evaluate a density-dependent matrix model to estimate recovery potential for lake sturgeon. The performance of the new model will be compared against Vélez-Espino and Koops's (2009) model and against a Ricker Model. The precautionary principle guides selection of a model that predicts populations and recovery times using the Namakan River lake sturgeon population as a case study for this region of Northern Ontario.

Model development

The Leslie Matrix predicts the population age structure at time t + 1 (N_{t+1}) by multiplying a projection matrix (M) and vector of age classes (N_t). The projection matrix takes the form of an NxNmatrix with the average fecundity for each age class along the top row, and the survival probability for each age class (Y) at N_y, N_{y+1}(Leslie 1948). This model can be modified into the Lefkovitch Matrix (Caswell 2001) to represent survival and fecundity on a yearly basis with ontogenetic stages of unequal duration, by changing the survival probability to the probability of survival and movement to the next stage at $N_y, N_{y+1}$and adding a diagonal representing the probability of survival and remaining in the same stage at N_y, N_y, as in Vélez-Espino and Koops (2008):

$$\begin{bmatrix} 0 & 0 & 0 & S_2G_2f_3 + S_3(1-G_3)f_3 & S_3G_3 + S_4f_4 \\ S_0 & S_1(1-G_1) & 0 & 0 & 0 \\ 0 & S_1G_1 & S_2(1-G_2) & 0 & 0 \\ 0 & 0 & S_2G_2 & S_3(1-G_3) & 0 \\ 0 & 0 & 0 & S_3G_3 & S_4 \end{bmatrix} \quad (1)$$

where S_n is the survival probability at stage n, $G_n$is the proportion of stage n that moves to the next stage, and f_n is the fecundity at stage n. Lake sturgeon only reproduce in the two adult stages (N_3 and N_4), fixing fecundity at 0 for larvae (N_0), juveniles (N_1), and subadults (N_2) Vélez-Espino and Koops (2009).

At its most basic, the Lefkovitch Model predicts a vector of the population structure at time t+1 (N_{t+1}) from the population at time t (N_t) and the projection matrix (M) using the formula:

$$N_{t+1} = [M]N_t \qquad (2)$$

A projection matrix representing only the growth of the population can be derived by subtracting the identity matrix (I) from M, giving the matrix model the form (Jensen 1995):

$$N_{t+1} = N_t + [M - I]N_t \qquad (3)$$

This form is equivalent to the exponential phase of growth in the logistic growth formula when the population is well below carrying capacity ($N \ll K$). A population-wide carrying capacity can be added to this model by multiplying the carrying-capacity term (*G*) by the growth term ($[M - I]N_t$), yielding the logistic density-dependent matrix model (Jensen 1995):

$$N_{t+1} = N_t + G[M - I]N_t \qquad (4)$$

where *G* is a scalar representing an adjustment to survival and fecundity across all stages based on the logistic growth equation.

While a population-wide carrying capacity could likely be determined for lake sturgeon using long-term datasets, this logistic form of the model does not adequately represent the role of density in stage-structured populations with separate carrying capacities at different life history stages. Lake sturgeon populations appear to be limited by density-dependent mortality during a five year long juvenile stage (Chapter 2). Cook and Leon (1976) propose a $2x2$ projection matrix with density-dependent elements, and Caswell and Takada (2004) modify this projection matrix with a Ricker model to determine juvenile survival. Density-dependent stages can be added to any NxN projection matrix by simply multiplying a density-dependent function by the survival or fecundity of any stage.

Materials and Methods

A density-dependent projection matrix for lake sturgeon

A density-dependent effect in lake sturgeon limited to five years (Chapter 2) may be due to a higher mortality for all individuals between years 0 and 5, or downward pressure from years 1 through 5 on age 0 fish trying to move into nursery habitat. For this chapter, I consider that density-dependent mortality is likely an effect on larval lake sturgeon experiencing higher mortality as they move into a densely populated nursery habitat. This assumption simplifies the model without changing the effect on post-recruitment individuals. I can produce a projection matrix by multiplying a density-dependent term by the survival at any point in the projection matrix (M).

In this case, I use a Ricker Model (Ricker 1954) to adjust the survival of larval (N_0) lake sturgeon based on a carrying capacity exclusive to larval (N_0) and juvenile (N_1) lake sturgeon. The Ricker Model is favoured over other forms of the logistic growth model because it does not predict negative growth when the population is much greater than the carrying capacity ($N \gg K$), an important feature in a species with larval production as high as that of the lake sturgeon. The new model takes the form:

$$\begin{bmatrix} 0 & 0 & 0 & S_2G_2f_3 + S_3(1-G_3)f_3 & S_3G_3 + S_4f_4 \\ S_0e^{1-\frac{N_1S_1+N_0S_0}{K^j}} & S_1(1-G_1) & 0 & 0 & 0 \\ 0 & S_1G_1 & S_2(1-G_2) & 0 & 0 \\ 0 & 0 & S_2G_2 & S_3(1-G_3) & 0 \\ 0 & 0 & 0 & S_3G_3 & S_4 \end{bmatrix} \tag{5}$$

A density-dependent form of equation 1 where K_j is the carrying capacity for juvenile lake sturgeon in the river. This has the effect of allowing the survival of age-0 lake sturgeon to vary from 0 to 2.7 times the basic larval survival rate (S_0), depending on the density of juvenile lake sturgeon.

Predicting equilibrium population structure

At equilibrium, a population is unaffected by fecundity and the number of juveniles (N_1) is fixed at a constant determined by the carrying capacity (K_j). This can be described by 4x4 projection matrix omitting the first row and first column, which describe fecundity and larval survival, and with the proportion of juveniles (N_1) at time t+1 fixed at 1:

$$\begin{bmatrix} 1 & 0 & 0 & 0 \\ S_1G_1 & S_2(1-G_2) & 0 & 0 \\ 0 & S_2G_2 & S_3(1-G_3) & 0 \\ 0 & 0 & S_3G_3 & S_4 \end{bmatrix} \tag{6}$$

The population structure (N) is a vector of length 4 composed of the population of juveniles (N_1), subadults (N_2), young adults (N_3), and old adults (N_4). Since $N_{t+1} = N_t$ at equilibrium, I modify Equation 3 to calculate the relationship between age classes, specifically setting the growth term equal to the zero vector:

$$[M - I]N_t = \underline{0} \qquad (7)$$

Population structure in the Namakan River

Vélez-Espino and Koops (2009) calculated the maximum reproductive age of lake sturgeon in the system by fitting the Von Bertalanffy (1938) growth equation to the length-age relationship of the system and setting the maximum age of reproduction to the age at which the Von Bertalanffy growth equation predicts as size of 95% of the maximum length attainable in the system (Appendix C). For this model, the adult stage was assumed to be all lake sturgeon older than age 24, a generalization of the age of maturation for females, and younger than the maximum reproductive age predicted for the system. This was further broken down by Vélez-Espino and Koops (2009) into two roughly equal length stages of young and old adults. The density of each stage class was determined from the age structure of Namakan System determined by Shaw (2008). Since no population estimate has been generated for the Namakan System, relationships can only be expressed between densities in this model. Density is expressed as the number of fish caught in the netting period between 2004 and 2008 per the total effort used in that sampling window.

Vélez-Espino and Koops (2009) similarly split the juvenile stage into two equal-length stages in their model. I adjusted the pre-adult stage into a juvenile stage to match ages 1 to 5 and a subadult stage to match ages 6 to 24. This has the effect of slightly increasing growth (λ) due to the movement of animals from a low survival stage to a higher survival stage earlier in life. Juvenile and subadult survival were calculated as in Vélez-Espino and Koops (2009). Annual adult mortality was estimated using catch-curve analysis by Shaw (2008) at 4.8%.

Shaw (2008) found that only individuals considered in this model to be adults were fully-recruited to the sampling gear, providing estimates only for the densities of adult lake sturgeon. The relatively constant mortality rate of adults in Shaw's dataset, along with the absence of particularly strong age classes, is suggestive that the population is either at or near equilibrium. I therefore calculate relative juvenile and subadult densities using Equation 7 and assuming that the Namakan System population is at equilibrium.

The modified matrix model calculates the effect of carrying capacity as age-0 fish move into the juvenile stage (Equation 5). As such, the equilibrium population of juvenile lake sturgeon alone is always below the juvenile carrying capacity and varies with larval survival. Further, Ricker density-dependent factors in matrix models tend to lead to overcompensation, where populations can overshoot carrying capacity and then return to it (Caswell and Takada 2004). The carrying capacity for juvenile lake sturgeon was separately computed using an iterative process by running the matrix model using the Ricker-modified larval survival term with the average larval survival for Canadian Designatable Unit 6 calculated by Vélez-Espino and Koops (2009).

Perturbation in nursery habitat

Since the equilibrium structure of all other stages is related to the equilibrium population of the density-dependent juvenile stage, I can predict that a reduction in juvenile carrying capacity (K_j) causes a proportional reduction in the equilibrium population of all other stages. The time necessary to reach equilibrium is determined in part by fecundity and larval survival. I computed the time to reach a new equilibrium and the new carrying capacity using a stochastic model, in which S_0 was allowed to vary around a normal distribution, with S_0 equal to the average larval survival computed by Vélez-Espino and Koops (2009) and a standard deviation of 25%. Ten runs of each model were performed, with K_j reduced by 25% and 50% from the equilibrium population structure and increased by 25% and 50%. This stochastic model was used to predict the recovery time of a population from an initial population of 10 young adult lake sturgeon, representing about 3% of the equilibrium adult population.

Relationship with the Ricker Model

Since the equilibrium stages are all proportional to each other, the adult population can be estimated at equilibrium using a Ricker Model, in which $K_a = N_3 + N_4$, and the reproductive rate can be estimated using the number of subadults per adult ($N_2 \div (N_3 + N_4)$) multiplied by the proportion of subadults that survive to the adult stage (S_2G_2), giving the following model:

$$N_{t+1(3,4)} = N_{t(3,4)} e^{N_{eq(2)} S_2 G_2 {N_{eq(3,4)}}^{-1} (1 - N_{eq(3,4)} {K_a}^{-1})} \qquad (8)$$

I fit this model to the Namakan River data to compare it with the recovery predicted by the stochastic model.

Results

Population structure

The maximum reproductive age of Namakan River lake sturgeon was calculated to be 47 years, making the adult stage 24- to 47-year-old lake sturgeon. The adult stage was consequently divided into a young adult stage from 24 to 36 years and an older adult stage from 37 to 47 years. Using the age distribution from Shaw (2008), I found that the density of young adults (N_3) was 252 and older adults (N_4) was 156. The starting density of subadults (N_2) was calculated to be 992, and juvenile density (N_1) was calculated to be 5973 (Equation 6). These were the initial conditions for the model. Stability was predicted from the current population conditions with a juvenile carrying capacity (K_j) of 7661 using an iterative process to find the value which led to stability. This value was rounded down to $K_j = 7000$ as a starting condition for the stochastic model to simplify the results.

Perturbation in Carrying Capacity

The equilibrium population of adult lake sturgeon changes proportionally to the juvenile carrying capacity (Figure 4.1). Under the initial conditions of the model, the equilibrium density of adults was 386. In all four scenarios, the stochastic model adjusted to a new equilibrium in between 17 and 25 years. It took a maximum of 42 years to reach a new equilibrium under predicted conditions from an initial density of 10 young adults (Table 4.1).

Table 4.1: Changes to the equilibrium population density of adult lake sturgeon ($N_3 + N_4$) with changes to the juvenile carrying capacity (K_j), and time to reach equilibrium predicted by the stochastic model. The initial equilibrium population density (N_{eq1}) is 386.

Scenario	Time to Equilibrium (years)	Magnitude of Change ($N_{eq1} - N_{eq2}$)
K_j decreased from 7000 to 3500	21	-273
K_j decreased from 7000 to 5250	17	-142
K_j increased from 7000 to 8750	20	+124
K_j increased from 7000 to 10500	25	+216
Recovery to $K_j = 7000$ from 10 young adults	42	+376

It took 42 years for the stochastic matrix model to recover from a population of 10 adult lake sturgeon to the maximum number of adult lake sturgeon predicted by the model. It took the pre-recruitment, naïve Ricker Model (Equation 8) 49 years to recover to 95% of the adult carrying capacity (Figure 4.2). The Ricker Model approached an equilibrium at the carrying capacity, where the stochastic model forecast an equilibrium slightly below the carrying capacity.

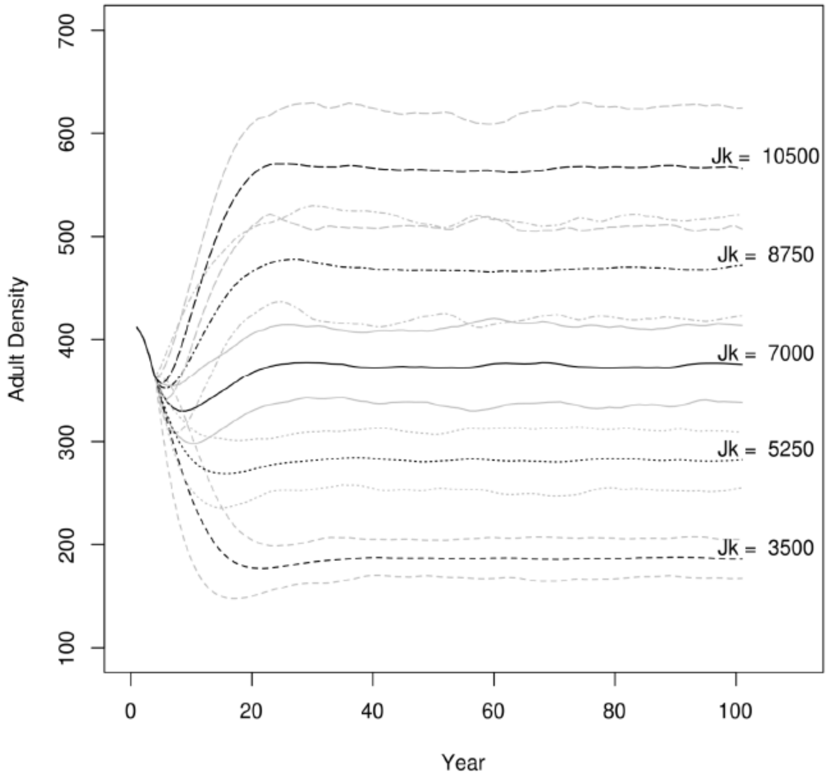


Figure 4.1: Simulated adult population density changes from the stochastic model under the same starting conditions with juvenile carrying capacities of 3500, 5250, 7000, 8750, and 10500. The adult equilibrium changes proportionally to the carrying capacity for juvenile lake sturgeon. Gray lines represent a 95% confidence interval for each model.

Discussion

Model suitability

The matrix model proposed by Vélez-Espino and Koops (2009) gives a good representation of recovery potential as a function of instantaneous growth rate. The elasticities in the model are conserved during the exponential growth phase of a density-dependent model and provide a useful approximation of the means by which

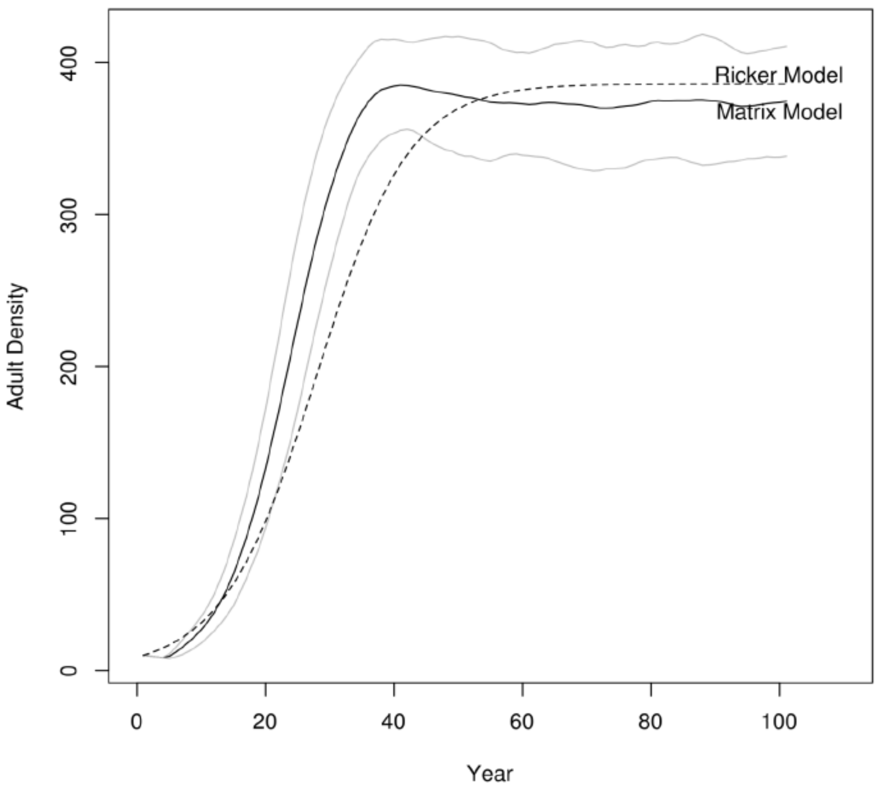


Figure 4.2: Recovery from 10 adult lake sturgeon in the stochastic model with juvenile carrying capacity, $K_j = 7000$ *(black line) and the naïve Ricker Model with adult carrying capacity,* $K_a = 386$*. Gray lines indicate the 95% confidence interval of the stochastic model. No confidence interval is given for the Ricker Model.*

adult populations can be increased relative to juvenile populations. Without a density-dependent term, however, the Vélez-Espino and Koops (2009) model does not realistically predict recovery over non-instantaneous time scales. Increasing post-recruitment survival may increase adult equilibrium populations relative to juvenile carrying capacities. In juvenile density limited systems, however, increasing and decreasing juvenile carrying capacities result in an outsized effect on the end-result of any recovery effort.

The density-limited matrix model that I propose in this chapter addresses the effect of juvenile density on recovery, even on stochastic systems. The model predicts population structures similar to what has been reported in the Namakan River case study and shows a predictable response to disturbances. The Ricker term, combined with the prolonged density independent phase, leads the model to be slightly overcompensating, with the effect overshooting the new carrying capacity in the direction of the change in all four scenarios, and then returning to an equilibrium. This effect may be caused by initially large stages spreading out through a multi-stage model. Increases and decreases in population size are relatively fast compared to the lifespan of the fish, with response times to disturbances that are generally less than the generation time of the population.

Recovery times and returns to equilibrium in the density-dependent matrix model were under 25 years for changes in the juvenile carrying capacity under 50% and under 50 years for complete recovery. This is consistent with the results from the Ricker Model, but shorter than the recovery times exceeding 60 years predicted using surplus production or density independent matrix models (Haxton et al. 2014, Vélez-Espino and Koops 2009).

The model generalizes the movement through stages by using a proportion of each stage that moves into the next stage each year derived from the annual survival of the stage divided by the number of years in the stage. It works well for extant populations but may overestimate the initial magnitude of a large disturbance because some proportion of each stage will move on to the next every year, regardless of whether any animals in that simulated stage were old enough to do so. This has an averaging effect on within-stage year-class strengths. This effect could be removed by a matrix model structured by year rather than stage, but the oldest lake sturgeon found in the Namakan System was 87 years old, and an 87 x 87 projection matrix could present additional challenges in parameter estimation and computation time.

Model predictions

Because all post-recruitment age classes are limited by mortality rates independent of density, the matrix model predicts an adult carrying capacity proportional to the juvenile carrying capacity. I can use the proportional survival of each stage to predict the stage structure knowing the density or population size of one or more stages. This is particularly helpful for estimating population sizes given that catchability in lake sturgeon varies with size.

The single-stage Ricker Model tracked the same population effects as the matrix model but took a longer time to reach equilibrium. This makes the Ricker Model preferable if the precautionary principle is applied. The difference is likely caused by the requirement in the Ricker model for the ratio between subadult and adult lake sturgeon to remain constant as the population varies. Recovering populations may have a much higher ratio of subadult to adult lake sturgeon, whereas declining populations may have a lower ratio of subadult to adult fish. This model may be useful for tracking population trends, but it requires knowledge of the ratio of subadult to adult lake sturgeon that cannot be obtained directly using density or catch-per-unit-effort estimates because lake sturgeon catchability varies with both size and stage. To obtain the constants used in this model, a census must be taken of adult and subadult fish, or the number of subadult fish must be estimated using the original matrix model.

Recommendations

In a system where density-dependent mortality occurs at any point in a species' life history, habitat management cannot easily be dismissed in calculations of recovery. The lake sturgeon's migratory life strategy lends itself to the presence of stage-specific recruitment bottlenecks, and it is important to include some analysis of these bottlenecks into predicting and managing population growth. A carrying capacity in the early life history of the species appears to limit the recruitment and, ultimately, population size of lake sturgeon in the Namakan River, and likely cause the same bottlenecks in other, similar, systems.

Density is likely a feature of river systems with limited habitat and may be most easily influenced by modifications to habitat. In this case, I might expect a fairly straightforward relationship between changes to available nursery habitat and changes to the carrying capacity for lake sturgeon in a given system. In the model, reducing carrying capacity for juveniles by half by reducing that habitat by half, predictably reduces the stable adult population by half. Conversely, increasing habitat and carrying capacity by half predictably increases stable adult populations by half. This relationship, however, may be an oversimplification of some effects relevant to management.

Lake sturgeon are similar in respect to a number of other species, including most anadromous salmonids and the Atlantic cod in the presence of a density-dependent bottleneck during the juvenile period prior to a density independent adult phase (Milner et al. 2003, Jonsson and Jonsson 1993, Chadwick 1982). A bottleneck can be detected in the age-structure of the adult population that cannot be explained by cyclical variations in spawning success (Chapter 2). Juveniles occupy nursery habitat distinct from the habitat used by adults (Chapter 3), lending the system to separate habitat effects between these life stages. This relationship is preserved even with substantial stochastic variation in larval survival (this chapter). The management implications of this life history structure are similar among most migratory and partially migratory fish, including salmonids and the Atlantic cod (Stiasny et al. 2016, Robillard et al. 2011, Milner et al. 2003, Jonsson and Jonsson 1993). Protection of juvenile nursery habitat could increase the lake sturgeon population in the Namakan System or enhance their recovery potential in similar rivers, while loss of nursery habitat could cause substantial declines in this population. The carrying capacity for adult lake sturgeon within the Namakan System is likely proportional to the available nursery habitat and consequently the available migratory distance for spawning adults, consistent with Auer's (1996a) findings for the Great Lakes.

Chapter 5: Discussion

The Problem

Lake sturgeon appear to follow an early life history strategy common among river migratory and partially migratory fishes. Adults spawn in high reaches of river systems and larvae migrate into nursery areas within their first year (Bruch et al. 2016, Bruch and Binkowski 2002, Auer 1999, Auer and Baker 2002). Maturation happens over several years, during which time subadult fish move from nursery areas into a behavioural regime consisting of habitat use and movements similar to those of adults. Sexual maturation appears to occur during this life history stage.

Juvenile lake sturgeon occupy distinct habitat from adult lake sturgeon and exhibit very small home range sizes in comparison (Trembath 2013, Barth et al. 2011, Haxton 2011, Beamish et al. 1998). Spatially restricted habitat in this life history stage increases risks associated with stochastic events (Thayer et al. 2017), and it is potentially vulnerable to increased population density in nursery habitat. A summary of the research reported here can be expressed as a separate carrying capacity (K_j) for juvenile lake sturgeon (Chapter 4). If vital rates are relatively unaffected by stochasticity, a population-wide carrying capacity (K) is established that is proportional to K_j. In this model, variations in K_j, such as those that might occur because of substantial changes in the availability of quality nursery habitat, can cause both declines and increases in the total population of lake sturgeon in systems like the Namakan River.

The model proposed in Chapter 4 is robust to stochasticity in reproductive rate and to highly variable mortality during the density-effected juvenile stage. In fact, the autocorrelative model that I use as a diagnostic test for the density effect requires some amount of stochasticity to be fit to an age-curve (Chapter 2). Variable spawning success, including occasional failed spawning years are included in the stochastic population model (Chapter 4), and do not substantially change the outcome of the model. This result is potentially troubling for management. Small populations, including those that are growing, can go extinct due to stochastic effects (Foley 1994). Lake sturgeon reproduce and mature slowly, making them potentially more vulnerable to catastrophes that may occur due to stochastic events at small population sizes.

Models

In this dissertation, I propose two models that relate density and life history in lake sturgeon. One model can be used to diagnose the presence and extent of a density bottleneck in the juvenile life history stage. The other is a population model that accounts for the species' complex life history strategy and separate carrying capacities for juvenile and adult stages.

Diagnostic Model

In Chapter 2, I applied Box and Jenkins's (1976) ARIMA model to age structure data to determine whether population density within a discrete life history stage affected lake sturgeon recruitment. This model uses autocorrelations and moving averages to relate a value in a time series to its previous values. The result of this modeling exercise was that any given year class of lake sturgeon was negatively impacted by the relative success of the four previous year classes. Given the species' stage-structured habitat use, it seems highly likely that this result indicates a density limitation within the juvenile stage. If a density limitation existed within the adult stage, the autocorrelation would be more pronounced and would fit the whole population. The larval phase lasts less than a year, and density effects within it would be undetectable in this model.

The lake sturgeon population in the Namakan Chain of Lakes represents an ideal case for fitting this particular model because the dominant factor in the catch curve derived from sampling this system is a relatively constant adult mortality. Nonetheless, the residuals of a simple mortality model did not meet the stationarity criteria for data to be used with ARIMA model. Thus, I used a first-order ARIMA model, a particular class of ARIMA model that should be robust to population data that have more random error or stronger unrelated trends. This model should be appropriate for catch curves from young, recovering populations, declining populations, and other unstable populations, provided that sufficient spawning occurs to keep the juvenile population near its carrying capacity (K_j) consistently during the lifetime of the oldest fish included in the model, and K_j does not change substantially during that time. The particular model that fit the Namakan Chain of Lakes lake sturgeon population best converges on constant annual recruitment over time, so fitting this model requires some degree of unexplained variation in the recruitment success, such as might occur when spawning success or larval survival varies due to stochastic effects.

Population models

In chapter 4, I propose a population model based on Vélez-Espino and Koops's (2009) matrix model. The new model accounts for a density-dependent effect limited to the juvenile life history stage. Its particular mode of action is to reduce the survival of larval lake sturgeon in proportion to how close the juvenile stage is to a theoretical juvenile carrying capacity. This model was run in a stochastic manner, allowing larval survival to vary based on both the density of juvenile lake sturgeon already in the system and a random survival rate that could, in nature, be caused by spawning failure, poor conditions for larvae, or other stochastic effects.

This matrix model was built assuming that lake sturgeon can be divided into five life history stages. For the purposes of this model, larval fish are considered to be all lake sturgeon within the first year of their lives. The juvenile stage is split into two intermediate stages, much like in Vélez-Espino and Koops's (2009) original model. For this model, however, I moved the transition point between young juveniles and subadults to year five to match the results of the model of density dependence in Chapter 2. I suggest that it is appropriate to model the length of the juvenile phase in every river system because the length of time that juveniles spend in nursery habitat before moving on to adult habitat could be very specific to a population, or even subpopulation, due to variations in environmental conditions between river systems, as well as in physiological adaptations to different habitat types. Maturation time in the species is known to vary with environmental conditions.

Future Work

The approach of using these two models to examine the effect of density at certain life history stages in lake sturgeon produces satisfactory results with the Namakan Chain of Lakes population. It also provides a framework for determining the temporal extent of the juvenile stage in similar populations.

A fair amount of work may fill some of the gaps that remain in this study. For instance, juvenile sampling herein provides some evidence of where juvenile lake sturgeon can be found in the Namakan River, but very little evidence of where they cannot be found. The extent of juvenile habitat, as well as some extensive suitability modeling could contribute some credibility to the mathematical model and literature-based assertion that juvenile habitat is limited.

Adult age distributions provide a long time series from limited sampling and help mitigate some of the effects of the size-related differences in catchability between different ages of lake sturgeon. The ARIMA model deals with much of the variation caused by short-run sampling of adult fish very well, but the effect of the mortality driven adult catch curve and errors associated with obtaining ages from fin-rays could be eliminated by constructing a time series from a long-term sampling effort focused entirely on juveniles. Additionally, such an effort would allow the observation of the effect of particularly large or small year classes as they move through the juvenile stage. Such data could be used to determine whether the observed density-dependent effect is the result of high juvenile densities disproportionately elevating mortality in settling young-of-the-year, if mortality is elevated by density disproportionately for certain year-classes, or if the density effect is evenly spread throughout the juvenile life history stage. Understanding the year-class structure of the juvenile stage is necessary to distinguish these effects and cannot be determined in the proposed model by inferring recruitment success from adult age distributions.

All of the relationships used in this dissertation were density-density, relating proportions of certain age classes in a sample to each-other. Consequently, the modified matrix model predicts the effect of changes to carrying capacity on the population of fish that would be caught in a theoretical sample identical to the one used. Expanding the sample using a measure of effort could be useful for management if relative population changes are all that is necessary but relating the model to an actual prediction of population size might be desirable. Census data generated from a mark-recapture survey or estimate of catchability could improve the usefulness of these models, although introducing errors associated with population estimates prior to calculating carrying capacities and vital rates should be avoided.

Bibliography

Aarts, G. MacKenzie, M., McConnel, B., Fedak, M., Matthiopoulos, J. (2008) Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* **31** (1), 140-160.

Adams, W. E., Kallemeyn, L. W., & Willis, D. W. (2006). Lake sturgeon population characteristics in Rainy Lake, Minnesota and Ontario. *Journal of Applied Ichthyology* **22**, 97-102.

Altenritter, M. E. L., Wieten, A. C., Ruetz, C. R. & Smith, K. M. (2013). Seasonal spatial distribution of juvenile lake sturgeon in Muskegon Lake, Michigan, USA. *Ecology of Freshwater Fish* **22**, 467-478.

Anderson, J. T. (1988). A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fishery Science*, **8**, 55-66.

Anderson, T. W. (2001). Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* **82** (1), 245-257.

Auer, N. A. (1996a). Importance of habitat and migration to sturgeons with emphasis on lake sturgeon. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**(S1), 152-160.

Auer, N. A. (1996b). Response of spawning lake sturgeons to change in hydroelectric facility operation. *Transactions of the American Fisheries Society*, **125**(1), 66-77.

Auer, N. A. (1999). Population characteristics and movements of lake sturgeon in the Sturgeon River and Lake Superior. *Journal of Great Lakes Research* **25** (2), 289-293.

Auer, N. A. & Baker, E. A. (2002). Duration and drift of larval lake sturgeon in the Sturgeon River, Michigan. *Journal of Applied Ichthyology* **18**, 557-564.

Barth, C. C. & Anderson, W. G. (2015). Factors influencing spatial distribution and growth of juvenile lake sturgeon (*Acipenser fulvescens*). *Canadian Journal of Zoology* **93** (11), 823-831.

Barth, C. C., Anderson, W. G., Peake, S. J. & Nelson, P. (2013). Seasonal variation in the diet of juvenile lake sturgeon, *Acipenser fulvescens*, Rafinesque, 1817, in the Winnipeg River, Manitoba, Canada. *Journal of Applied Ichthyology* **29** (4), 721-729.

Barth, C. C., Anderson, W. G., Henderson, L. M., & Peake, S. J. (2011). Home range size and seasonal movement of juvenile lake sturgeon in a large river in the Hudson Bay drainage basin. *Transactions of the American Fisheries Society* **140** (6), 1629-1641.

Barth, C. C., Peake, S. J., Allen, P. J. & Anderson, W. G. (2009). Habitat utilization of juvenile lake sturgeon, *Acipenser fulvescens*, in a large Canadian river. *Journal of Applied Ichthyology* **25**, 18.

Beamesderfer, R. C. P. & Farr, R. A. (1997). Alternatives for the protection and restoration of sturgeons and their habitat. *Environmental Biology of Fishes* **48**, 407-417.

Beamish, F. (1979). Migration and spawning energetics of the anadromous sea lamprey, *Petromyzon marinus*. *Environmental Biology of Fishes* **4** (1), 3-7.

Beamish, F., Noakes, D. & Rossiter, A. (1998). Feeding ecology of juvenile Lake Sturgeon, *Acipenser fulvescens*, in Northern Ontario. *Canadian Field-Naturalist* **112** (3), 459-468.

Bennion, D. H. & Manny, B. A. (2014). A model to locate potential areas for lake sturgeon spawning habitat construction in the St. Clair-Detroit River System. *Journal of Great Lakes Research* **40** (2), 43-51.

Benson, A. C., Sutton, T. M., Elliot, R. F., Meronek, T. G. (2005). Seasonal movement patterns and habitat preferences of age-0 lake sturgeon in the lower Peshtigo River, Wisconsin. *Transactions of the American Fisheries Society*. 134, 1400-1409.

Bezold, J. & Peterson, D. L. (2008). Assessment of lake sturgeon reintroduction in the Coosa River System, Georgia-Alabama. *In* M. Allen, S. Sammons & M. Maceina, *Balancing Fisheries Management and Water Uses for Impounded River Systems,* Vol. 62 Pp. 571-586. (ISBN: 978-1-934874-06-6.)

Billard, R., & Lecointre, G. (2000). Biology and conservation of sturgeon and paddlefish. *Reviews in Fish Biology and Fisheries*, **10**(4), 355-392.

Boase, J. C., Manny, B. A., Donald, K. A. L., Kennedy, G. W., Diana, J. S., Thomas, M. V. & Chiotti, J. A. (2014). Habitat used by juvenile lake sturgeon (*Acipenser fulvescens*) in the North Channel of the St. Clair River (Michigan, USA). *Journal of Great Lakes Research* **40** (2), 81-88.

Boudreault, F. R., Dupont, J. N., Sylvain, C. (1977). Modèles linéaires de prédiction des débarquements de homard aux Iles-de-la-Madeleine (Golfe du Saint-Laurent). *Journal of the Fisheries Research Board of Canada* **34** (3), 379-383.

Borkholder, B. D., Morse, S. D., Weaver, H. T., Hugill, R. A., Linder, A. T., Schwarzkopf, L. M., Perrault, T. E., Zacher, M. J. & Frank, J. A. (2002). Evidence of a year-round resident population of lake sturgeon in the Kettle River, Minnesota, based on radiotelemetry and tagging. *North American Journal of Fisheries Management* **22** (3), 888-894.

Bouckaert, E. K., Auer, N. A., Roseman, E. F. & Boase, J. (2014). Verifying success of artificial spawning reefs in the St. Clair-Detroit River System for lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817). *Journal of Applied Ichthyology* **30** (6, SI), 1393-1401.

Box, G. E., & Jenkins, G. M. (1976). *Time series analysis: forecasting and control, revised ed.* Holden-Day.

Bruch, R. (1999). Management of lake sturgeon on the Winnebago System - long term impacts of harvest and regulations on population structure. *Journal of Applied Ichthyology* **15** (4-5), 142-152.

Bruch, R. M. & Binkowski, F. P. (2002). Spawning behavior of lake sturgeon (*Acipenser fulvescens*). *Journal of Applied Ichthyology* **18**, 570-579.

Bruch, R. M., Campana, S. E., Davis-Foust, S. L., Hansen, M. J. & Janssen, J. (2009). Lake sturgeon age validation using bomb radiocarbon and known-age fish. *Transactions of the American Fisheries Society* **138** (2), 361-372.

Bruch, R. M., Haxton, T. J., Koenigs, R., Welsh, A., & Kerr, S. J. (2016). Status of lake sturgeon (*Acipenser fulvescens* Rafinesque 1817) in North America. *Journal of Applied Ichthyology*, **32** (S1), 162-190.

Caroffino, D. C., Sutton, T. M., Elliott, R. F. & Donofrio, M. C. (2010). Early life stage mortality rates of lake sturgeon in the Peshtigo River, Wisconsin. *North American Journal of Fisheries Management* **30** (1), 295-304.

Caroffino, D. C., Sutton, T. M., Elliot, R. F., & Donofrio, M. C. (2011). Predation on early life stages of Lake Sturgeon in the Pestigo River, Wisconsin. *Transactions of the American Fisheries Society* **139** (6), 1846-1856.

Caswell, N., Peterson, D., Manny, B. & Kennedy, G. (2004). Spawning by lake sturgeon (*Acipenser fulvescens*) in the Detroit River. *Journal of Applied Ichthyology* **20** (1), 1-6.

Caswell, H. & Takada, T. (2004). Elasticity analysis of density-dependent matrix models: the invasion exponent and its substitutes. *Theoretical Population Biology* **65** (4), 401-411.

Chadwick, E. M. P. (1982). Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. *Canadian Journal of Fisheries and Aquatic Sciences* **39** (11), 1496-1501.

Chiasson, W., Noakes, D. & Beamish, F. (1997). Habitat, benthic prey, and distribution of juvenile lake sturgeon (*Acipenser fulvescens*) in northern Ontario rivers. *Canadian Journal of Fisheries and Aquatic Sciences* **54** (12), 2866-2871.

Chiotti, J. A., Holtgren, J. M., Auer, N. A. & Ogren, S. A. (2008). Lake sturgeon spawning habitat in the Big Manistee River, Michigan. *North American Journal of Fisheries Management* **28** (4), 1009-1019.

Cooke, D. & Leon, J. (1976). Stability of population growth determined by a 2 x 2 Leslie matrix with density-dependent elements. *Biometrics* **32** (2), 435-442.

Crossman, J., Forsythe, P., Baker, E. Scribner, K. (2009). Overwinter survival of stocked age-0 lake sturgeon. *Journal of Applied Ichthyology* **25** (5), 516-521.

Crossman, J., Forsythe, P., Scribner, K. & Baker, E. (2011). Hatchery rearing environment and age affect survival and movements of stocked juvenile lake sturgeon. *Fisheries Management and Ecology,* **18**, 132-144.

Damstra, R. A. & Galarowicz, T. L. (2013). Summer habitat use by lake sturgeon in Manistee Lake, Michigan. *Transactions of the American Fisheries Society,* **142** (4), 931-941.

Daugherty, D. J., Sutton, T. M., & Elliott, R. F. (2009). Suitability modelling of lake sturgeon habitat in five northern Lake Michigan tributaries: implications for population rehabilitation. *Restoration Ecology*, **17** (2), 245-257.

Deegan, L.A. (1993). Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. *Canadian Journal of Fisheries and Aquatic Sciences* **50** (1), 74-79.

Dieterman, D. J., Frank, J., Painovich, N. & Staples, D. F. (2010). Lake sturgeon population status and demography in the Kettle River, Minnesota, 1992-2007. *North American Journal of Fisheries Management* **30** (2), 337-351.

Dumont, P., D'Amours, J., Thibodeau, S., Dubuc, N., Verdon, R., Garceau, S., Bilodeau, P., Mailhot, Y. & Fortin, R. (2011). Effects of the development of a newly created spawning ground in the Des Prairies River (Quebec, Canada) on the reproductive success of lake sturgeon (*Acipenser fulvescens*). *Journal of Applied Ichthyology* **27** (2), 394-404.

Duke, S. Anders, P., Ennis, G., Hallock, R., Hammond, J. Ireland, S., Laufle, J., Lauzier, R., Lockhard, L., Martoz, B., Paragamian, V. L., Westerhof, R. (1999). Recovery plan for Kootenai River white sturgeon (*Acipenser transmontanus*). *Journal of Applied Ichthyology* **15**, 157-163

Espinoza, M., Farrugia, T. J., Webber, D. M., Smith, F. & Lowe, C. G. (2011). Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. *Fisheries Research* **108** (2-3), 364.

Ferguson, M. & Duckworth, G. (1997). The status and distribution of lake sturgeon, *Acipenser fulvescens*, in the Canadian provinces of Manitoba, Ontario and Quebec: A genetic perspective. *Environmental Biology of Fishes* **48** (1-4), 299-310.

Foley, P. (1994). Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology* **8** (1), 124-137.

Forsythe, P. S., Scribner, K. T., Crossman, J. A., Ragavendran, A., Baker, E. A., Davis, C. & Smith, K. K. (2012). Environmental and lunar cues are predictive of the timing of river entry and spawning-site arrival in lake sturgeon *Acipenser fulvescens*. *Journal of Fish Biology* **81** (1), 35-53.

Forsythe, P. S., Scribner, K. T., Crossman, J. A., Ragavendran, A., Baker, E. A. (2013). Experimental assessment of the magnitude and sources of lake sturgeon egg mortality. *Transactions of the American Fisheries Society* **142**(4), 1005-1011.

Fortin, R., Dumont, P., Guenette, S. (1996). Determinants of growth and body condition of lake sturgeon (*Acipenser fulvescens*). *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 1150-1156.

Friday, M. J. (2011). The migratory and reproductive response of spawning lake sturgeon to controlled flows over Kakabeka Falls on the Kaministiquia River, 2011. Unpublished report, Ontario Ministry of Natural Resources and Forestry.

Gardiner, B. G., Schaeffer, B., Masserie, J. A. (2005) A review of the lower actinopterygian phylogeny. *Zoological Journal of the Linnean Society* **144** (4), 511-525.

Gerig, B., Moerke, A., Greil, R. & Koproski, S. (2011). Movement patterns and habitat characteristics of Lake Sturgeon (*Acipenser fulvescens*) in the St. Mary's River, Michigan, 2007-2008. *Journal of Great Lakes Research* **37** (2, SI), 54-60.

Gross, M. R., Repka, J., Robertson, C. T., Secor, D. H., & Van Winkle, W. (2002). Sturgeon conservation: insights from elasticity analysis. *American Fisheries Society Symposium* **28**, 13-30.

Hare, A. J., Waheed, A. & Anderson, W. G. (2015). Cortisol and catecholamine responses to social context and a chemical alarm signal in juvenile lake sturgeon, *Acipenser fulvescens*. *Canadian Journal of Zoology* **93** (8), 605-613.

Harkness, W. J. K., & Dymond, J. R. (1961). The lake sturgeon: the history of its fishery and problems of conservation. Fish & Wildlife Branch, Ontario Department of Lands and Forests.

Haxton, T., Friday, M., Cano, T., Hendry, C. (2015). Assessing the magnitude of effect of hydroelectric production on lake sturgeon abundance in Ontario. *North American Journal of Fisheries Management* **35** (5), 930-941.

Haxton, T. (2011). Depth selectivity and spatial distribution of juvenile lake sturgeon in a large, fragmented river. *Journal of Applied Ichthyology* **27** (2), 45-52.

Haxton, T., Whelan, G. & Bruch, R. (2014). Historical biomass and sustainable harvest of Great Lakes lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817). *Journal of Applied Ichthyology* **30** (6, SI), 1371-1378.

Haxton, T. J. & Findlay, C. S. (2008). Variation in lake sturgeon (*Acipenser fulvescens*) abundance and growth among river reaches in a large regulated river. *Canadian Journal of Fisheries and Aquatic Sciences* **65** (4), 645-657.

Hay-Chmielewski, E. M., & Whelan, G. E. (1997). Lake sturgeon rehabilitation strategy. Michigan Department of Natural Resources, Fisheries Division Special Report Number 18, Ann Arbor, MI, USA.

Hixon, M. A., & Carr, M. H. (1997). Synergistic predation, density dependence, and population regulation in marine fish. *Science* **277** (5328), 946-949.

Holbrook, S. J. & Schmitt, R. J. (2002). Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology* **83** (10), 2855-2868.

Holtgren, J. & Auer, N. (2004). Movement and habitat of Juvenile Lake Sturgeon (*Acipenser fulvescens*) in the Sturgeon river/portage lake system, Michigan. *Journal of Freshwater Ecology* **19** (3), 419-432.

Houston, J. J. (1987). Status of the lake sturgeon, *Acipenser fulvescens*, in Canada. *Canadian Field-Naturalist* **101** (2), 171-185.

Hrenchuk, C. L., McDougall, C. A., Nelson, P. A., & Barth, C. C. (2017) Movement and habitat use of juvenile Lake Sturgeon (*Acipenser fulvescens*, Rafinesque, 1817) in a large hydroelectric reservoir (Nelson River, Canada). *Journal of Applied Ichthyology.* **30**, 1-16.

Jacobs, G. R., Bruestle, E. L., Hussey, A., Gorsky, D., Fisk, A. T. (2016). Invasive species alter ontogenic shifts in the trophic ecology of lake sturgeon (*Acipenser fulvescens*) in the Niagara River and Lake Ontario. *Biological Invasions* **19**, 1533-1546.

Jensen, A. L. (1997). Matrix population model with density-dependent recruitment for assessment of age-structured wildlife populations. *Bulletin of Mathematical Biology*, **59**(2), 255-262.

Johnson, J. H., LaPan, S. R., Klindt, R. M. & Schiavone, A. (2006). Lake sturgeon spawning on artificial habitat in the St Lawrence River. *Journal of Applied Ichthyology* **22** (6), 465-470.

Jonsson, B., & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* **3**, 348-365.

Kallemeyn, L. W. (1987). Correlations of regulated lake levels and climatic factors with abundance of young-of-the-year walleye and yellow perch in four lakes in Voyageurs National Park. *North American Journal of Fisheries Management* **7**, 513-521.

Kaeser, A. J. & Litts, T. L. (2010). A novel technique for mapping habitat in navigable streams using low-cost side scan sonar. *Fisheries* **35** (4), 163.

Kempinger, J. J. (1988). Spawning and early life history of lake sturgeon in the Lake Winnebago system, Wisconsin. *American Fisheries Society Symposium* **5** (1), 12-122.

Kessel, S. T., Hondorp, D. W., Holbrook, C. M., Boase, J. C., Chiotti, J. A., Thomas, M. V., Willis, T. C., Roseman, E. F., Drouin, R. & Krueger, C. C. (2018). Divergent migration within lake sturgeon (*Acipenser fulvescens*) populations: multiple distinct patterns exist across an unrestricted migration corridor. *Journal of Animal Ecology* **87**, 259-273.

Krishnamoorthy, K. & Thomson, J. (2004). A more powerful test for comparing two Poisson means. *Journal of Statistical Planning and Inference* **119**, 23-35.

Lallaman, J. J., Damstra, R. A. & Galarowicz, T. L. (2008). Population assessment and movement patterns of lake sturgeon (*Acipenser fulvescens*) in the Manistee River, Michigan, USA. *Journal of Applied Ichthyology* **24** (1), 1-6.

Logan-Chesney, L. M., Dadswell, M. J., Karsten, R. H., Wirgin, I. & Stokesbury, M. J. W. (2018). Atlantic sturgeon *Acipenser oxyrinchus* surfacing behaviour. *Journal of Fish Biology* **Early view** DOI: 10.1111/jfb.13552.

Lyons, J. & Stewart, J. S. (2014). Predicted effects of future climate warming on thermal habitat suitability for Lake Sturgeon (*Acipenser fulvescens*, Rafinesque, 1817) in rivers in Wisconsin, USA. *Journal of Applied Ichthyology* **30** (6), 1508-1513.

Maceina, M. J. (2004). Verifying residuals from catch curves to detect recruitment variation in largemouth bass and crappies. *North American Journal of Fisheries Management* **24** (1), 231-236.

Martin, A. D., Quinn, K. M. & Park, J. H. (2011). Mcmcpack: Markov chain Monte Carlo in R. *Journal of Statistical Software* **42** (9).

McCabe, D. J., Beekey, M. A., Mazloff, A. & Marsden, J. E. (2006). Negative effect of zebra mussels on foraging and habitat use by lake sturgeon (*Acipenser fulvescens*). *Aquatic Conservation-Marine and Freshwater Ecosystems* **16** (5), 493-500.

McLeod, D. & Martin, C. (2015). Movement and seasonal distribution of lake sturgeon in the Namakan River, Ontario. 2007 to 2013 Completion Report. *Fort Frances District Report Series 94*. Ontario Ministry of Natural Resources and Forestry.

McDougall, C. A., Blanchfield, P. J. & Anderson, W. G. (2014). Linking movements of lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) in a small hydroelectric reservoir to abiotic variables. *Journal of Applied Ichthyology* **30** (6), 1149-1159.

McDougall, C. A., Hrenchuk, C. L., Anderson, W. G. & Peake, S. J. (2013). The rapid upstream migration of pre-spawn lake sturgeon following trap-and-transport over a hydroelectric generating station. *North American Journal of Fisheries Management* **33** (6), 1236-1242.

McIntosh, A. R., & Peckarsky, B. L. (2004). Are mayfly anti-predator responses to fish odour proportional to risk? *Archiv für Hydrobiologie*, **160** (2), 145-151.

Merriman, J. C., Anthony, D. H. J., Kraft, J. A. & Wilkinson, R. J. (1991). Rainy River water quality in the vicinity of bleached kraft mills. *Chemosphere* **23** (11), 1605-1615.

Milner, N. J., Elliott, J. M., Armstrong, J. D., Gardiner, R., Welton, J. S., & Ladle, M. (2003). The natural control of salmon and trout populations in streams. *Fisheries Research*, **62** (2), 111-125.

Myers, R. A., Barrowman, N. J., Hutchings, J. A. & Rosenberg, A. A. (1995). Population dynamics of exploited fish stocks at low population levels. *Science* **269** (5227), 1106.

Nichols, J. S., Kennedy, G., Crawford, E., Allen, J., French, J., Black, G., Blouin, M., Hickey, J., Chernyák, S., Haas, R. & Thomas, M. (2003). Assessment of lake sturgeon (*Acipenser fulvescens*) spawning efforts in the Lower St. Clair River, Michigan. *Journal of Great Lakes Research* **29** (3), 383.

Nielsen, J. L., Arrizabalaga, H., Fragoso, N., Hobday, A., Lutcavage, M. & Sibert, J.Gezelius, S. S. & Raakjaer, J., (ed.). (2009). *Tagging and Tracking of Marine Animals with Electronic Devices, Vol. 9.* Springer, 452 pages.

Nilo, P., Tremblay, S., Bolon, A., Dodson, J., Dumont, P. & Fortin, R. (2006). Feeding ecology of juvenile lake sturgeon in the St. Lawrence river system. *Transactions of the American Fisheries Society* **135** (4), 1044-1055.

Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. (2008). State-space models of individual animal movement. *Trends in Ecology & Evolution* **23** (2), 87-94.

Peterson, D. L., Vecsei, P., & Jennings, C. A. (2007). Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. *Reviews in Fish Biology and Fisheries*, **17** (1), 59-76.

Pollock, M. S., Carr, M., Kreitals, N. M. & Phillips, I. D. (2015). Review of a species in peril: what we do not know about lake sturgeon may kill them. *Environmental Reviews* **23** (1), 30-43.

QGIS Development Team (2009). QGIS Geographic Information System. Open Source Geospatial Foundation.

R Development Core Team (2008). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing (ISBN 3-900051-07-0). Retrieved from http://www.r-project.org.

Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Board of Canada* **11**(5), 559-623.

Robillard, M. M., Casselman, J. M., McLaughlin, R. L., & Mackereth, R. W. (2011) Alternative growth histories in populations of Lake Superior brook trout: critical support for partial migration. *Biological Conservation* **144** (7), 1931-1939.

Rossiter, A., Noakes, D. L. G. & Beamish, F. W. H. (1995). Validation of age estimation for the lake sturgeon. *Transactions of the American Fisheries Society* **124**, 777-781.

Rusak, J. A. & Mosindy, T. (1997). Seasonal movements of lake sturgeon in Lake of the Woods and the Rainy River, Ontario. *Canadian Journal of Zoology* **75** (3), 383-395.

Sakamoto, K., Dew, W. A., Hecnar, S. J. & Pyle, G. G. (2016). Effects of lampricide on olfaction and behavior in young-of-the-year lake sturgeon (*Acipenser fulvescens*). *Environmental Science and Technology* **50** (7), 3462-3468.

Secor, D. H., Anders, P. J., Van Winkle, W., & Dixon, D. A. (2002). Can we study sturgeons to extinction? What we do and don't know about the conservation of North American sturgeons. *American Fisheries Society Symposium* **28**, 3-10.

Shaw, S. L. (2010). Lake sturgeon *(Acipenser fulvescens)* population attributes, reproductive structure and distribution in Namakan Reservoir, Minnesota and Ontario. M.Sc. Thesis, South Dakota State University, Brookings, South Dakota.

Shaw, S. L., Chipps, S. R., Windels, S. K., Webb, M. A. H. & McLeod, D. T. (2013). Influence of sex and reproductive status on seasonal movement of lake sturgeon in Namakan Reservoir, Minnesota-Ontario. *Transactions of the American Fisheries Society* **142** (1), 10-20.

Shaw, S. L., Chipps, S. R., Windels, S. K., Webb, M. A. H., McLeod, D. T. & Willis, D. W. (2012). Lake sturgeon population attributes and reproductive structure in the Namakan Reservoir, Minnesota and Ontario. *Journal of Applied Ichthyology* **28** (2), 168-175.

Sloychuk, J. R. (2015). Life-skills training for juvenile lake sturgeon (*Acipenser fulvescens*). M.Sc. Thesis, University of Saskatchewan, Saskatoon, Canada.

Smith, K. & Baker, E. (2005). Characteristics of spawning lake sturgeon in the Upper Black River, Michigan. *North American Journal of Fisheries Management* **25** (1), 301-307.

Smith, K. & King, D. (2005). Movement and habitat use of yearling and juvenile lake sturgeon in Black Lake, Michigan. *Transactions of the American Fisheries Society* **134** (5), 1159-1172.

Sowa, V. A. (2002). Steep Rock Iron Mines: Dredging and draining of Steep Rock Lake and some of the effects after 45 years. Pages 393-402 *in* Proceedings, Ninth International Conference on Tailings and Mine Waste, Colorado State University, Fort Collins.

Stergiou, K. I. (1991). Short-term fisheries forecasting: comparison of smoothing, ARIMA and regression techniques. *Journal of Applied Ichthyology* **7** (4), 193-204.

Stiasny M., Mittermayer F., Sswat M., Voss R., Jutfelt F., Chierici M., Puvanendran V., Mortensen A., Reusch T., Clemmesen C. (2016) Ocean acidification effects on Atlantic cod larval survival and recruitment to the fished population. *PloS One*. **11**(8) e0155448.

Sutton, A. D. (1997). Lake Sturgeon Rehabilitation Strategy. State of Michigan Department of Natural Resources. Fisheries Division. Special Report 18.

Tessier, J. (2015). Classification of riverbed substrate in a juvenile lake sturgeon nursery area on the Namakan River, Rainy River District, Ontario. H.B.Sc. Thesis, Lakehead University, Thunder Bay, Canada.

Thayer, D., Ruppert, J. L. W., Watkinson, D., Clayton, T., Poesch, M. S. (2017). Identifying temporal bottlenecks for the conservation of large-bodied fishes: lake sturgeon (*Acipenser fulvescens*) show highly restricted movement and habitat use over-winter. *Global Ecology and Conservation* **10**, 194-205.

Thiem, J. D., Binder, T. R., Dawson, J. W., Dumont, P., Hatin, D., Katopodis, C., Zhu, D. Z. & Cooke, S. J. (2011). Behaviour and passage success of upriver-migrating lake sturgeon *Acipenser fulvescens* in a vertical slot fishway on the Richelieu River, Quebec, Canada. *Endangered Species Research* **15** (1), 1.

Thiem, J. D., Dawson, J. W., Gleiss, A. C., Martins, E. G., Haro, A., Castro-Santos, T., ... & Cooke, S. J. (2015). Accelerometer-derived activity correlates with volitional swimming speed in lake sturgeon (*Acipenser fulvescens*). *Canadian Journal of Zoology* **93** (8), 645-654.

Thiem, J. D., Hatin, D., Dumont, P., Van Der Kraak, G. & Cooke, S. J. (2013). Biology of lake sturgeon (*Acipenser fulvescens*) spawning below a dam on the Richelieu River, Quebec: behaviour, egg deposition, and endocrinology. *Canadian Journal of Zoology* **91** (3), 175-186.

Trembath, C. A. (2013). An assessment of juvenile lake sturgeon movement and habitat use in the Namakan River of Northwestern Ontario. M.Sc.F. Thesis, Lakehead University, Thunder Bay, Canada.

Trested, D. G., Chan, M. D., Bridges, W. C. & Isely, J. J. (2011). seasonal movement and mesohabitat usage of adult and juvenile lake sturgeon in the Grasse River, New York. *Transactions of the American Fisheries Society* **140** (4), 1006-1014.

Tsitsika, E. V., Maravelias, C. D., & Haralabous, J. (2007). Modeling and forecasting pelagic fish production using univariate and multivariate ARIMA models. *Fisheries Science* **73** (5), 979-988.

Vélez-Espino, L. A. & Koops, M. A. (2009). Recovery Potential Assessment for Lake Sturgeon in Canadian Designatable Units. *North American Journal of Fisheries Management* **29** (4), 1065-1090.

Wang, Y. L., Binkowski, F. P. & Doroshov, S. I. (1985). Effect of temperature on early development of white and lake sturgeon, *Acipenser transmontanus* and *A. fulvescens*. *Environmental Biology of Fishes* **14**(1), 43-50.

Waraniak, J., Valentine, S. & Scribner, K. (2017) Effects of changes in alternative prey densities on predation of drifting lake sturgeon larvae (*Acipenser fulvescens*). *Journal of Freshwater Ecology* **32** (1), 619-632.

Warth, P., Hilton, E. J., Naumann, B., Olsson, L. & Konstantinidis, P. (2018). Development of the muscles associated with the mandibular and hyoid arches in the Siberian sturgeon, *Acipenser baerii* (Acipenseriformes: Acipenseridae). *Journal of Morphology* **279**, 163-175.

Welsh, A. B. & McLeod, D. T. (2010). Detection of natural barriers to movement of lake sturgeon (*Acipenser fulvescens*) within the Namakan River, Ontario. *Canadian Journal of Zoology* **88** (4), 390-397.

Wishingrad, V., Carr, M. K., Pollock, M. S., Ferrari, M. C. O. & Chivers, D. P. (2014a). Lake Sturgeon Geographic Range, Distribution, and Migration Patterns in the

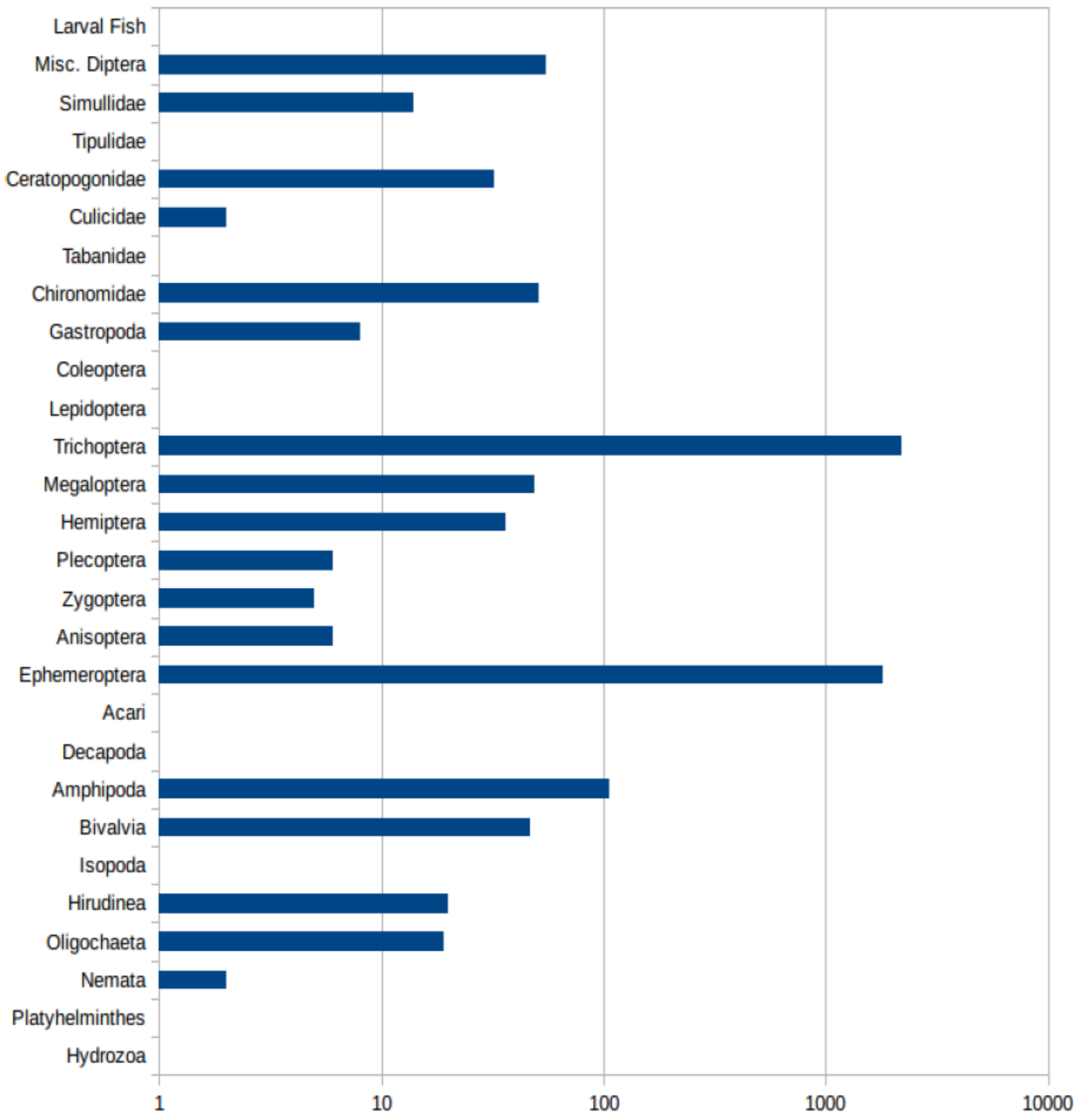
Saskatchewan River. *Transactions of the American Fisheries Society* **143** (6), 1555-1561.

Wishingrad, V., Sloychuk, J. R., Ferrari, M. C. O. & Chivers, D. P. (2014b). Alarm cues in Lake Sturgeon Acipenser fulvescens Rafinesque, 1817: potential implications for life-skills training. *Journal of Applied Ichthyology* **30** (6), 1441-1444.

Appendix A: Confirmed spawning sites in the Namakan River from the 2013, 2014, 2015, and 2016 spawning seasons

Out of respect for the Lac La Croix community's help on this project as well as a mutual desire to protect the Namakan River lake sturgeon population from poaching, the contents of this appendix are covered by a non-disclosure agreement between the Lac La Croix First Nation, Ontario Ministry of Natural Resources and Forestry, and Lakehead University. This information is not to be included in the publicly available version of this document. For more information contact myself or Brian McLaren.

Appendix B: Diet of juvenile lake sturgeon captured in Bill and Threemile Lakes.



Appendix C: Von Bertalanffy growth curve for lake sturgeon in the Namakan System.

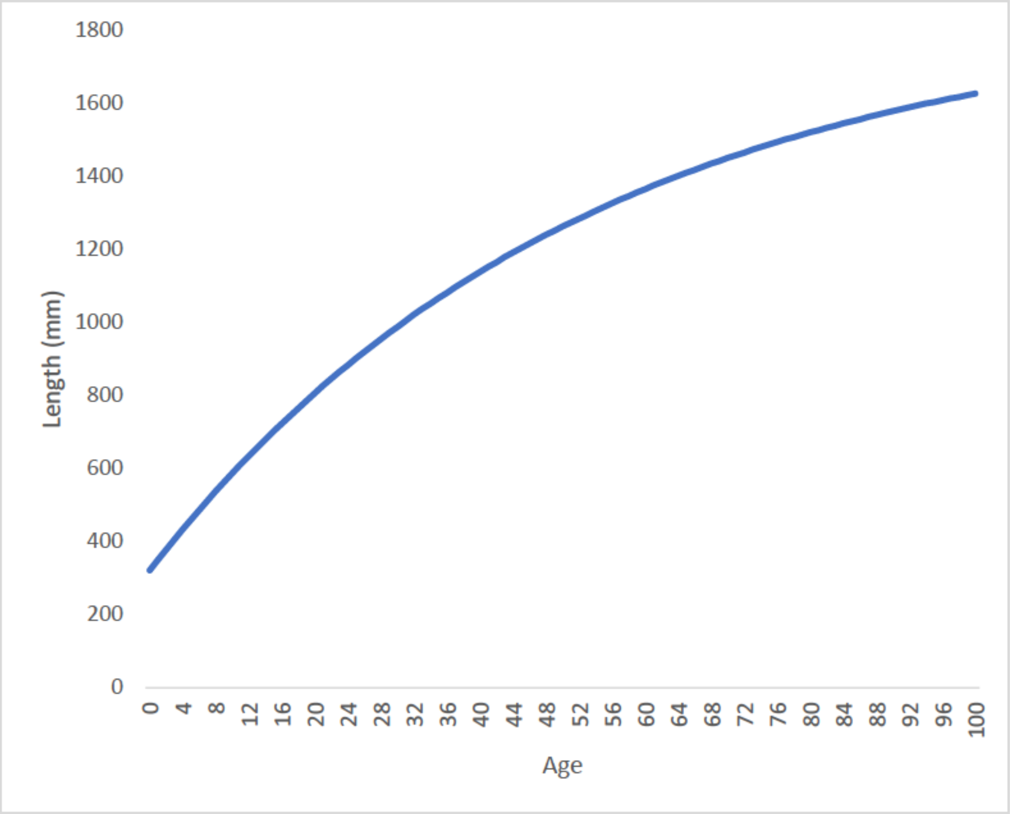


Figure C.1: The von Bertalanffy growth curve for adult lake sturgeon captured in the Namakan River from 2004 to 2008 (Shaw 2010).

Appendix D: Length-weight relationship, capture locations, and age distributions for adult lake sturgeon captured in the Namakan River and Chain of Lakes 2004 to 2013.

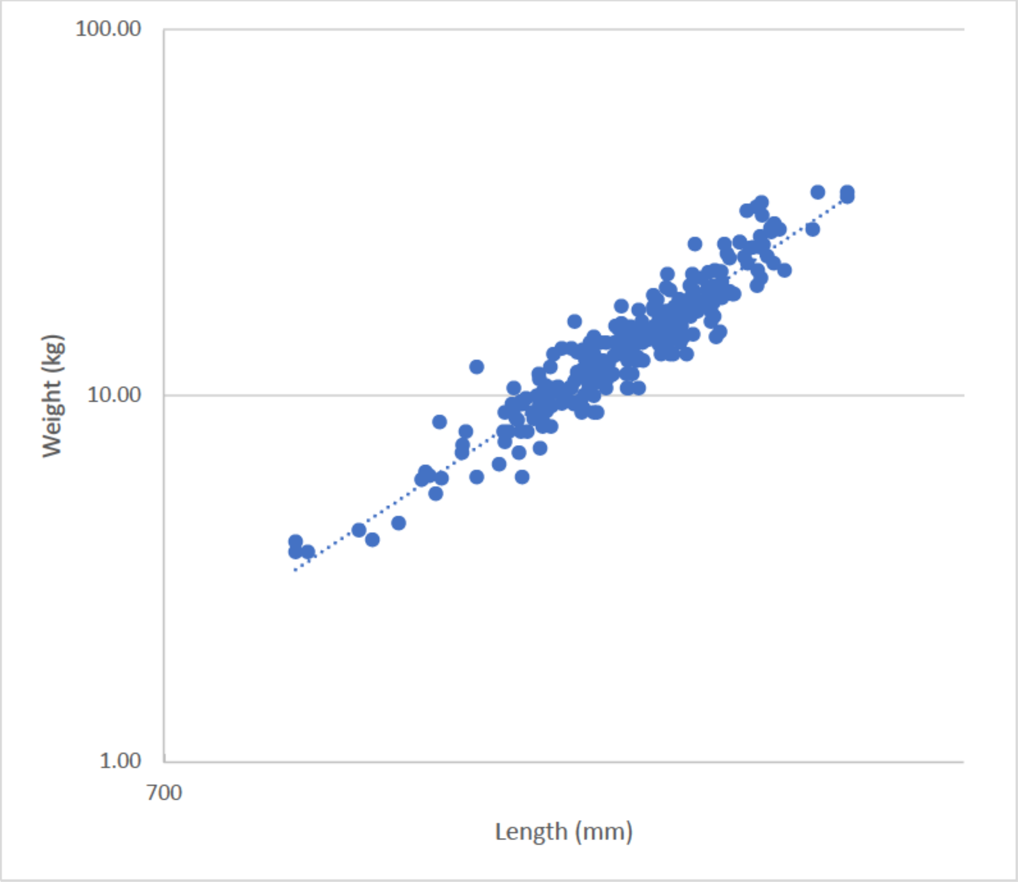


Figure D.1: Total length-weight ratio for lake sturgeon captured between 2004 and 2008 in the Namakan Chain of Lakes plotted on a log-log scale. Total lengths ranged from 832 to 1715 mm. Weights ranged from 3.75 to 36 kg n=266. Weights were not taken for Namakan River Captures.

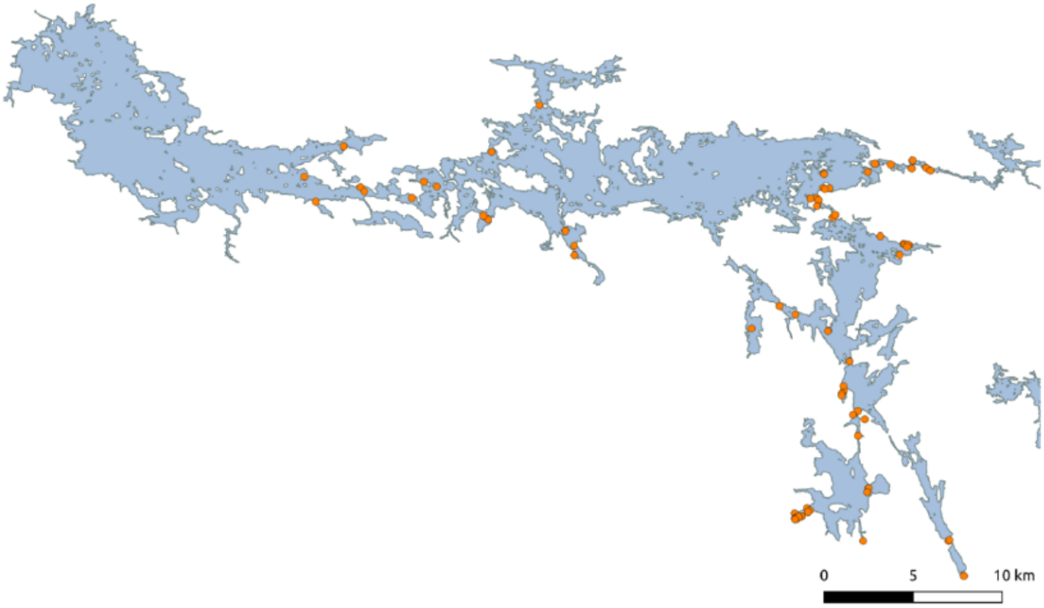
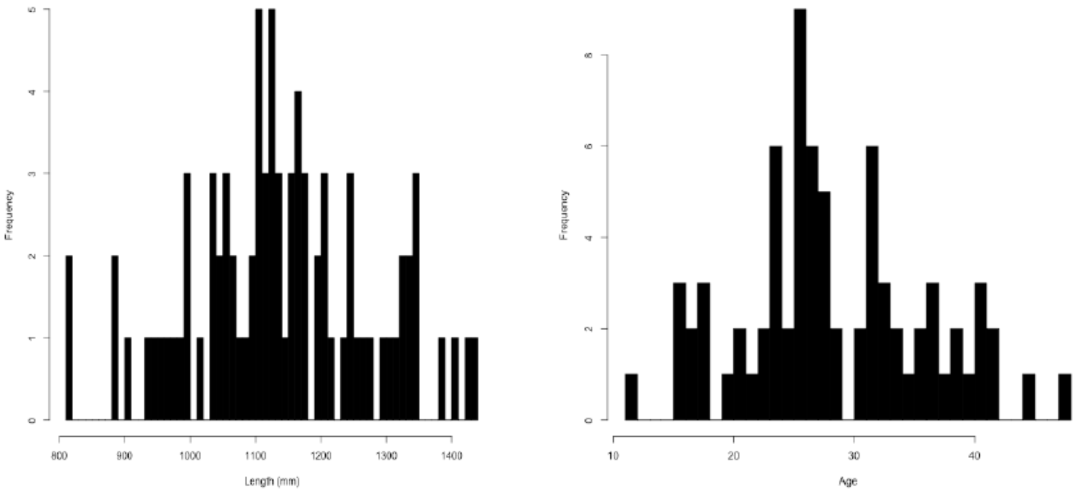


Figure D.2: Capture locations for adult lake sturgeon captured in the Namakan Chain of Lakes 2004-2012.



(a)

(b)

Figure D.3: Length-frequency (a) and age-frequency charts for captures conducted in the Namakan River in 2012 and 2013 and Namakan Chain of Lakes in 2012. N=83.