

**Spawning habitat and reproductive strategies of lake
trout (*Salvelinus namaycush*) in a northern boreal lake**

By

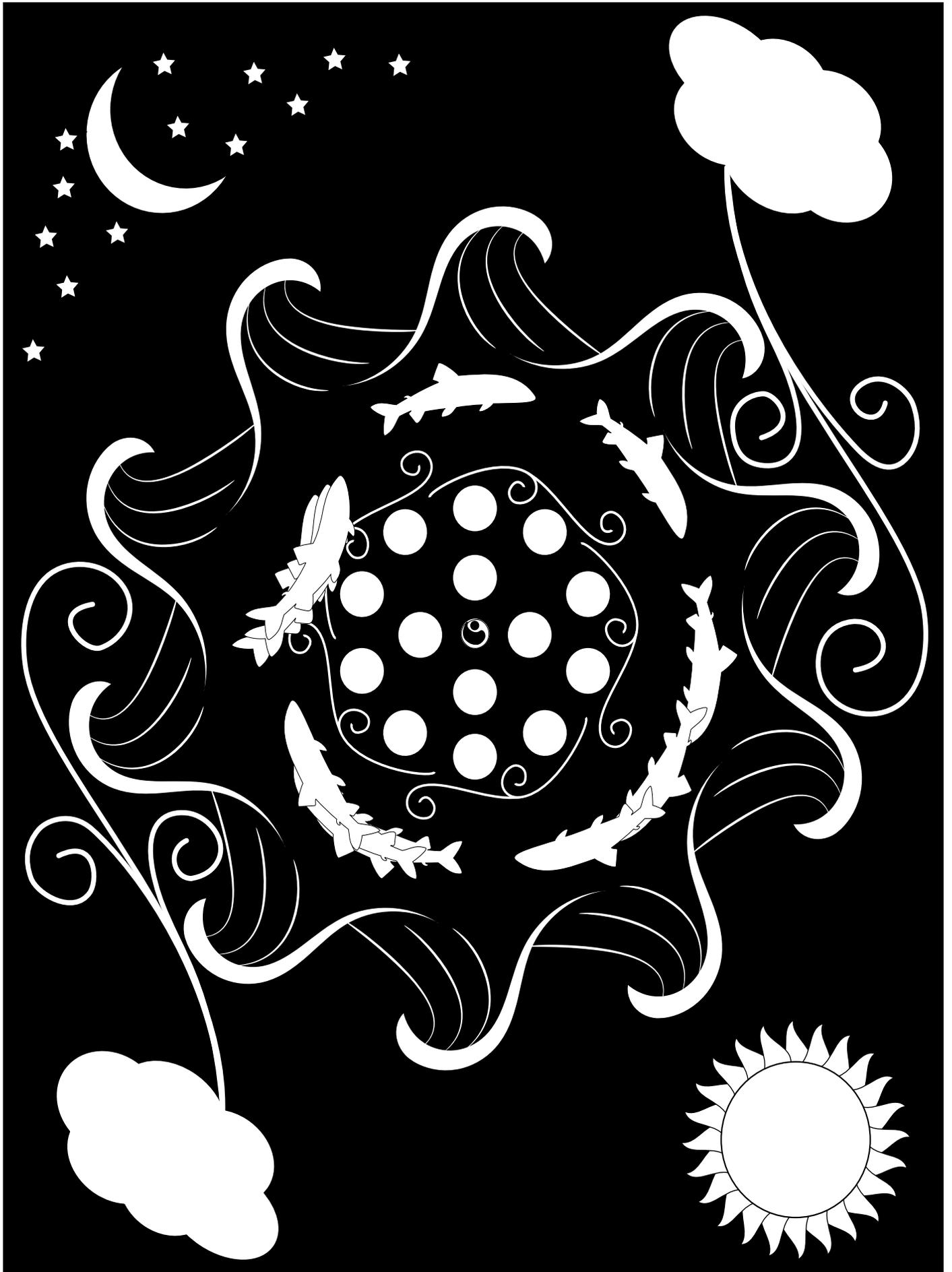
David T. Callaghan

A Thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba
in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

Department of Biological Sciences
University of Manitoba
Winnipeg

Copyright © 2016 by David T. Callaghan



Abstract

Lake trout (*Salvelinus namaycush*) have a broad distribution across Canada's north, yet most studies that describe reproductive habitat and behaviour have been conducted in the southern extent of their range. Northern regions are experiencing unprecedented changes from climate and industrial development, and thus there is a pressing need to understand the reproductive habitat and behaviour of this species. I examined a dozen sites around Alexie Lake, Northwest Territories, to test if physical habitat and wind exposure were important determinants of spawning site use and embryonic survival. Spawning was found to occur in ~2 m water depth, on 3–15 cm diameter clean substrate on the leading edge of shoals that ended in a rock crib rising abruptly in nearshore regions around the lake. Wind direction was predominantly from the west, although it was highly variable within and among spawning seasons. I found evidence of lake trout spawning at each site examined, which was not limited to shoals facing a predominant wind direction. High variation in embryonic survival (2–83%) from incubation trays was observed among spawning sites, demonstrating a large gradient in habitat quality exists within a given lake. However, modelled wind exposure did not predict embryonic survival, nor did physical characteristics - including shoal depth and slope, as well as cobble size and shape - that may influence interstitial water flow on spawning shoals.

Using an acoustic telemetry monitoring system and novel spatial temporal clustering analysis, I was able to quantify lake trout spawning movements and behaviours

over the course of an entire spawning season. Lake trout formed clusters on spawning shoals around the entire nearshore region, as well as around several islands, confirming that suitable spawning habitat is abundant in Alexie Lake. Males arrived on spawning shoals earlier than females and remained longer for a maximum of 25 consecutive days; females occupied spawning shoals for a maximum of 8 consecutive days over the course of the spawning season. Males formed over four times as many spawning clusters and visited twice as many sites than females. Spawning clusters were predominantly formed at night but were also observed during daylight hours, especially during the peak spawning season (September 9–19). I found males had higher activity rates, and spent longer periods on spawning shoals, than females, in spite of similar daily travel distances between sexes. Overall, my findings challenge the conventional role of wind as a predominant predictor of lake trout spawning site quality. I propose that the unpredictable nature of wind and abundance of suitable habitat may favour lake-wide spawning by lake trout as a bet-hedging strategy in northern lakes with limited fetch.

Acknowledgements

I thank my supervisor Dr. Paul Blanchfield, who took on a close-minded fish enthusiast with a love for snorkeling and opened my eyes to the world of telemetry. Supporting me to attend conferences, workshops and courses in Canada, U.S.A. and Germany, as well as encouraging me to explore new data analyses to broaden my analytical skills is greatly appreciated.

I thank my committee members for their time and feedback on my thesis. In particular I would like to thank: Dr. Peter Cott for his advice in the field, I will always remember to keep my hands warm during winter sampling; Dr. Micheline Manseau for providing ideas on movement analyses and for introducing me to spatial temporal clustering; Dr. James Hare for your positive energy during committee meetings.

I am very grateful to Matt Guzzo, Lee Hrenchuk, Kristen Patterson, A.J. Chapelsky, Francios Larouche, Jessica Mai and Alex Wall for their help with project logistics and with fieldwork. Scott Milne for hydroacoustic work. Dr. Trevor Pitcher for providing incubation trays used in my egg incubation experiment. Zahid Hossain and Dr. Pourang Irani for showing how powerful spatial temporal clustering can be as a visual tool for animal movement. Diego for your love and companionship on several field trips, one cannot understate the value of a loyal camp dog to keep the squirrels at bay.

Thank you to my family and friends for their support of my academic endeavours and to Kerri for her encouragement, understanding and patience over the course of my Master's thesis.

The project was funded by DeBeers Canada (Paul J. Blanchfield and Peter A. Cott), Fisheries and Oceans Canada, NSERC Strategic Grant 430655-12 (Paul J. Blanchfield), and additional support from the W. Garfield Weston Award for Northern Research.

Table of Contents

Abstract	ii
Acknowledgements	iv
Chapter 1: Introduction	1
<i>1.1 General Introduction</i>	<i>1</i>
<i>1.2 Reproductive strategies of Salmonine fishes</i>	<i>1</i>
<i>1.3 Lake trout reproductive strategies</i>	<i>4</i>
<i>1.4 Northern development</i>	<i>7</i>
<i>1.5 Objectives</i>	<i>7</i>
Chapter 2: Lake trout (<i>Salvelinus namaycush</i>) spawning habitat in a northern lake: the role of wind and physical characteristics on habitat quality*	9
<i>2.1 Introduction</i>	<i>10</i>
<i>2.2 Methods</i>	<i>13</i>
2.2.1 Study site	13
2.2.2 Spawning habitat	15
2.2.3 Wind data collection and wind exposure modelling	16
2.2.4 Embryonic survival	19
2.2.5 Statistical analysis	21
<i>2.3 Results</i>	<i>22</i>
2.3.1 Spawning habitat	22
2.3.2 Wind	25
2.3.3 Wind exposure model	27
2.3.4 Embryonic survival	28
	vi

<i>2.4 Discussion</i>	31
Chapter 3: Lake Trout Reproductive Strategies	40
<i>3.1 Introduction</i>	41
<i>3.2 Methods</i>	44
3.2.1 Study Site	44
3.2.2 Lake water temperature	46
3.2.3 Lake bathymetry	46
3.2.4 Fish acoustic telemetry	47
3.2.5 Acoustic telemetry data filter	48
3.2.6 Movement metrics	49
3.2.7 Spatial temporal clustering analysis	49
3.2.8 Spawning activity determined by cluster filtering	50
3.2.9 Spawning cluster metrics	51
3.2.10 Statistical analysis	52
<i>3.3 Results</i>	53
3.3.1 Spatial distribution of lake trout	53
3.3.2 Spatial distribution of spawning clusters	56
3.3.3 Timing of spawning	56
3.3.4 Lake trout spawning behaviour	65
<i>3.4 Discussion</i>	69
Chapter 4: Conclusions	75
Literature Cited	79
Appendix	92
<i>Spatial Error Evaluation</i>	96

<i>Spatial Temporal Cluster Analysis</i>	99
<i>References</i>	109

Table of Figures

- Figure 2.1 – The locations of 12 spawning sites (S1-S12) sampled in Alexie Lake, NWT. The bathymetric contours (grey lines) are at 10 m increments. The locations of the temperature logger string (circle containing an x) and weather station (triangle) are indicated.** 14
- Figure 2.2 – Profile of a typical Alexie Lake, NWT, spawning shoal (left). Three zones are depicted from offshore to nearshore: the silt zone located offshore before the drop-off; the rock crib located at the drop off where spawning occurs; and the sand and silt zone towards the shoreline. A photograph depicts a sampling hoop and ruler during habitat sampling on a typical spawning shoal in Alexie Lake.** 23
- Figure 2.3 – a) Kernel density estimate of substrate size for selected lake trout spawning sites in Alexie Lake, NWT (see Fig. 1), and (b) cumulative proportion distributions of substrate size for each spawning site. Dashed lines represent the minimum (3 cm) and maximum (15 cm) spawning substrate size used by lake trout (Martin and Olver, 1980). The solid line represents the mean (8.9 cm) substrate size in Alexie Lake.** 24
- Figure 2.4 –Relative frequency of wind direction and related wind speed prevailing during three consecutive lake trout spawning seasons (September 19 to October 1, 2012; September 1 to October 1, 2013; September 1 to 29, 2014) at Alexie Lake, NWT, are expressed as wind roses. Radii represent 10-degree bins.** 26
- Figure 2.5 – Modelled estimates of wind exposure at 12 lake trout spawning sites in Alexie Lake, NWT (see Fig. 1). Bars represent the proportion of wind speeds that result in water currents (i.e. $\geq 3.3 \text{ m s}^{-1}$) at each site during three consecutive spawning seasons (2012 black; 2013 dark grey; 2014 light grey).** 30
- Figure 3.1 – Alexie Lake is located 30 km Northeast of Yellowknife, NWT. The bathymetric contours are at 10 m increments.** 45

- Figure 3.2 – Depth distribution of males (A) and females (B) during the spawning season in Alexie Lake, NWT. The black line represents the 15° C isocline. Points were given transparency value of 5%, therefore the darker the colour the higher the density of points. No data are available between September 25-27, 2013, while the VPS was removed from the lake for download. 54**
- Figure 3.3 – Kernel density estimate of bottom contour depth occupied by male (blue) and female (red) lake trout in Alexie Lake, NWT, between August 30 and September 30, 2013. 55**
- Figure 3.4 – Kernel density estimate (KDE) of distance to nearest shore occupied by male (blue) and female (red) lake trout in Alexie Lake, NWT, between August 30 and September 30, 2013. 57**
- Figure 3.5 – Male (blue), and female (red) lake trout positions during the 2013 spawning season in Alexie Lake, NWT. Points were given transparency value of 10%, therefore the darker the colour the higher the density of points 58**
- Figure 3.6 – Lake trout spawning clusters in Alexie Lake, NWT during the 2013 spawning season. The smaller red circles represent the center of high activity clusters and larger blue circles represent the center of low activity clusters 60**
- Figure 3.7 – Spawning cluster formation by individual lake trout in Alexie Lake, NWT. Squares represent one or more spawning cluster formed on the date for males (blue) and females (red) and vertical black lines represent the onset and conclusion of peak spawning. 60**
- Figure 3.8 – Frequency distribution of spawning clusters over the duration of the 2013 spawning season in Alexie Lake, NWT. Light grey bars represent the cumulative frequency of spawning clusters (both low and high activity), dark grey bars represent high activity spawning clusters, the horizontal black line represents daily surface water temperature (°C) and the vertical black lines represent the onset and conclusion of peak spawning. 62**
- Figure 3.9 – Frequency distributions of male (blue) and female (red) spawning clusters over the duration of the 2013 spawning season in Alexie Lake, NWT. Light bars represent**

daily cumulative frequency of spawning clusters (both low and high activity), dark bars represent high activity spawning clusters and vertical black lines represent the onset and conclusion of peak spawning. 63

Figure 3.10 – Lake trout spawning cluster formation start times over the duration of the 2013 spawning season (left panel), and summarized as total counts per hour (right panel), in Alexie Lake, NWT. Both low activity (open circles) and high activity (closed circles) are displayed in both panels. Light grey polygons represent dawn and dusk, dark grey polygons represent nighttime and vertical black lines represent the onset and conclusion of peak spawning. The lines in the right panel represent a LOESS trendline with 95% confidence interval error bars. 64

Figure A1 – VEMCO VR2W acoustic receiver and reference tag positions in Alexie Lake, NWT. 93

Figure A.2 – Stationary tag trial positions (red circles) in Alexie Lake, NWT, on 12 known spawning shoals 95

Figure A.3 – Mobile tag test in Alexie Lake, NWT. Each line colour represents a separate mobile trial. Filled circles represent the start position and filled squares represent at the finish position of each trial. 97

Figure A.4 – 2DRMS of binned HPE’s relationship to measurement error. Red triangles represent 2DRMS of binned HPE, black points represent data points, blue dashed line represents the segmented regression line, vertical black lines represent the breakpoints in the segmented regression. 100

Figure A.5 – 2DRMS of binned HPE’s relationship to measurement error. Red triangles represent 2DRMS of binned HPE, black points represent data points, dashed line represents the linear model $y = 0.18x + 7.9$. 101

Figure A.6 – Example of a sorted k-distance plot for the 10th nearest neighbour. The solid line represents the data and the dashed line represents the parameter estimate 102

Figure A.7 – Kernel density estimate (black line) for measurement error of a mobile tag trial in the x coordinate. The red line represents the best fit distribution (log-normal) used to generate x measurement error in the simulations. 104

Figure A.8 – An example of overlap between error clusters (red) and real clusters (blue) of simulated tracks (black line and dots) after error is added to each point (red line and dots). 105

Figure A.9 – Summary graph of cluster simulations to determine the maximum allowable 2DRMS HPE filter for the cluster analysis. Ratio represents the mean ratio of error clusters to real clusters, Overlap represents the mean overlap of real clusters by error clusters, Missed represents the mean percent of real clusters with no overlap of error clusters, Overhang represents mean percent area of error clusters that overhang the area of real clusters, and Phantom represent mean percent of error clusters with no overlap of real clusters. 106

Table of Tables

- Table 2.1 – Parameter estimates of quasibinomial generalized linear model on the global model for predicting embryonic survival. The explanatory variables included wind exposure (wind), spawning shoal slope (slope), depth of embryo incubator (depth), mean length of substrate (length), and mean shape of substrate (shape). Residual deviance: 2.81 on 6 degrees of freedom. QAICc ranked the null model (intercept only) as the top model describing embryonic survival.** 32
- Table 3.1 – Summary statistics for spawning male, spawning female and non-spawning female lake trout movement metrics during the 2013 spawning season in Alexie Lake, NWT. I report the number of fish (n), means and standard deviations of daily distance travelled (km), persistence index (PI), and acceleration ($m s^{-2}$).** 67
- Table 3.2: Summary statistics for male and female lake trout spawning cluster data during the 2013 spawning season in Alexie Lake, NWT. For all male and female clusters (both high and low activity clusters) and spawning male and female clusters (high activity clusters), I report the number of fish (n), means and standard deviations of clusters formed, cluster duration, unique cluster sites visited, distance between consecutive clusters (m), duration between subsequent clusters (h), site visits prior to first spawn and minimum convex polygon area of all cluster points (km^2).** 68
- Table A.1 – 2DRMS HPE filter summary statistics for cluster simulations to determine the maximum allowable 2DRMS HPE filter for the cluster analysis. The table showcases no HPE filter and 27 m 2DRMS HPE filter, as well as mean \pm SD and optimum values for 27 to 15 m 2DRMS HPE Filters. Ratio represents the mean ratio of error clusters to real clusters, Overlap represents the mean overlap of real clusters by error clusters, Missed represents the mean percent of real clusters with no overlap of error clusters, Overhang represents mean percent area of error clusters that overhang the area of real clusters, and Phantom represent mean percent of error clusters with no overlap of real clusters.**

Chapter 1: Introduction

1.1 General Introduction

A vast array of reproductive strategies are employed by various species across the animal kingdom. The evolution of animal mating systems is largely influenced by sexual selection (Andersson, 1994), parental care (Trivers, 1972) and the spatiotemporal distribution of resources and mates (Emlen and Oring, 1977). Reproductive strategies will ultimately reflect the number of mates an individual acquires per breeding season, conflicts between the two sexes and the resolution of such conflict (Berglund, 1997). In many animal species, males optimize fitness benefits through mating with multiple females; by contrast, a female's optimal reproduction rate is limited by the production of progeny (Bateman, 1948). The increased energetic investment in gametes by females often result in conventional sex roles whereby females provide parental care and males compete for access to females (Kokko and Jennions, 2008). Ultimately mating systems are shaped by the distribution in time and space of resources necessary for each sex to ensure successful reproduction (Emlen and Oring, 1977).

1.2 Reproductive strategies of Salmonine fishes

The salmonines (subfamily Salmoninae) include salmons, trouts and chars of the genera *Oncorhynchus*, *Salmo* and *Salvelinus*. The diversity of life history traits within the salmonines has prompted the evolution of highly variable intraspecific mating systems.

Some examples include: semelparous versus iteroparous breeding (Crespi and Teo, 2002; Fleming, 1998); fall versus spring spawning (Groot and Margolis, 1991); migratory versus resident populations (Fleming, 1998); and the evolution of male alternative reproductive tactics (Gross, 1985; Healey and Prince, 1998; Koseki and Maekawa, 2000). This breadth of reproductive strategies along with within-system diversity, such as partial migration where a population contains both migratory and resident individuals (Jonsson and Jonsson, 1993), make salmonines an ideal group of fishes to investigate the relative influence of sexual selection, parental care and spatiotemporal resource availability on reproductive success.

With such intraspecific diversity among salmonines, I will briefly describe the characteristics that generalize their mating system as a group. Salmonines spawn on clean, silt-free gravel beds in cold and well-oxygenated freshwater streams, rivers or along lakeshores (Esteve, 2005; Groot and Margolis, 1991). Intergravel water movement is a primary requirement for salmonine egg incubation because fertilized eggs are typically buried in gravel substrate and left unattended to hatch several months later (Becker and Neitzel, 1985; Chapman, 1988). For most salmonine species, females select appropriate sites and excavate a series of pits (termed a redd) in which they successively deposit and bury their eggs (de Gaudemar, 1998). The limited number of suitable spawning sites and variability in spawning site quality results in females becoming very selective when choosing their redd sites (Blanchfield and Ridgway, 2005; de Gaudemar, 1998; Esteve, 2005). Males compete for access to females, which is thought to be the limiting resource for male reproduction (Gross, 1984), while females compete for territories to establish their redds (Fleming, 1998). During spawning males and females

emit their gametes simultaneously with their bodies vibrating against each other directly over the redd (Esteve, 2005). Females can spawn with many males in a single spawning act or with different males in successive acts (Garant et al., 2001). Males maximize reproductive success quantitatively, by mating with as many females as possible; whereas females maximize reproductive success qualitatively, by choosing appropriate redd sites and quality males (de Gaudemar, 1998). Overall, salmonine reproductive strategies result in a polygamous system in which sexual selection, parental care and the spatiotemporal availability of resources influence their mating systems.

Males arrive earlier (Morbey, 2000) and stay longer on the spawning grounds than females (Fleming, 1996). Competition among males for access to females may result in dominance hierarchy formation (Keenleyside and Dupuis, 1998). Body size is typically the main factor in establishing dominance during fighting, with larger males defeating smaller ones, but other factors may also affect the outcome of agonistic interactions. Some of the most elaborate sexual dimorphism is seen in the Pacific salmon (*Oncorhynchus* spp.) where they develop bright colouration, hooked snouts, large hooked lower jaws (kype) and humped backs (Vladykov, 1962). These secondary sexual characteristics are a product of the semelparous life history of most Pacific salmon where individuals invest all of their effort into a single reproduction season, which is ultimately followed by death (de Gaudemar, 1998). This life history strategy promotes intense competition among males for access to females, and among females for access to spawning habitat. The same sexually selected traits (i.e. develop bright colouration, hooked snouts, large hooked lower jaws (kype) and humped backs), which are valued by females, will also enhance mating success through female choice (Dugatkin and

FitzGerald, 1997; Fisher, 1958). The high cost of fighting and agonistic displays has led to male alternative strategies and tactics within the salmonine group (Gross, 1996).

Depending on the age of maturation, salmonine males can adopt three strategies: mature as older, younger, or precocious males (Esteve, 2005). In addition, salmonine males can employ two tactics to achieve fertilizations; either they fight to maintain position next to the female, or sneaking towards the females vent and depositing their sperm (Gross, 1984). This is evident in Atlantic salmon, *Salmo salar*, where older males compete for dominance and develop exaggerated weaponry (kype), which is also selected more readily by females (Fleming, 1996). Younger males can either search for females not defended by larger males and fight for dominance, take up a satellite position behind a large male and fight for lead position among other satellite males, or employ a sneaker tactic. Precocious males (parr) are smaller and tend to employ a sneaker strategy for reproductive success (Fleming, 1998, 1996).

1.3 Lake trout reproductive strategies

Lake trout (*Salvelinus namaycush*) are iteroparous lake-spawners. During the fall, lake trout migrate onto spawning shoals (Gunn, 1995). The spawning time generally coincides with surface water temperatures declining to 12° C or lower (Redick, 1967). Preferred spawning habitat is selected along exposed shorelines off points, islands or on mid-lake shoals (Martin and Olver, 1980). These shoals typically face prevailing winds and are often close to deep water (Royce, 1951). Spawning substrate is usually clean and consists of cobble, broken rubble or angular rock mainly 3-15 cm in diameter along with dispersed boulders (Martin and Olver, 1980). Most spawning shoals are less than 6 m deep (Martin and Olver, 1980), but can range from 0.15 m in Squam Lake (Merriman,

1935) to 91 m in Lake Superior (Eschmeyer, 1955). No parental care is given to eggs other than the careful selection of spawning habitat by females (Redick, 1967). Males arrive earlier on breeding grounds and stay longer than females each year (Martin and Olver, 1980; Miller and Kennedy, 1948; Muir et al., 2012; Royce, 1951). Males also mature earlier and are more likely to spawn annually leading to a highly skewed operational sex ratio with males constituting from 60–85 % of the spawning population (Eschmeyer, 1955; Martin, 1957; Miller and Kennedy, 1948). Lake trout appear to show a size-based spawning phenology with smaller lake trout spawning earlier than larger lake trout (Martin, 1957; Miller and Kennedy, 1948; Royce, 1951). Mate choice is cryptic or absent as both sexes appear to spawn promiscuously (Esteve et al., 2008). Environmental, physiological and behavioural triggers of lake trout reproduction, spawning site selection, reproductive strategies and mate choice are still largely unknown (Muir et al., 2012).

Reproductive behaviours of lake trout contrast sharply with the general salmonine mating system (Esteve et al., 2008; Gunn, 1995; Muir et al., 2012). First, spawning usually takes place on wave-swept shoals of lakes without building a redd (Martin and Olver, 1980). Second, lake trout show no apparent male-male agonistic behaviour (Esteve et al., 2008; Gunn, 1995; Royce, 1951), a predominant behavioural characteristic in the Salmoninae subfamily (Esteve, 2005). Third, females do not show territorial behaviour (i.e. redd defence) or obvious mate selection (Esteve et al., 2008). Fourth, lake trout express some extent of sexual dimorphism (males develop dark lateral banding) but not nearly as pronounced as other salmonines (Martin and Olver, 1980). Finally, spawning predominately occurs during the night (Gunn, 1995).

Wind events appear to play a definitive role in lake trout reproduction (Muir et al., 2012). Currents induced by wind events can be beneficial to egg incubation by removing fine sediments from the interstitial areas where eggs are deposited and replenishing these areas with oxygenated water (Gunn, 1995; Sly, 1988). Due to the dynamic nature of wind and its likely benefits to egg incubation, habitat quality may vary spatially and temporally throughout the course of a breeding season, as well as among years. The extent to which wind influences lake trout egg survival is not fully understood and requires further investigation.

Reproductive strategies of females are presumably driven by habitat quality; with females selecting appropriate sites of high quality to incubate eggs (de Gaudemar, 1998; Muir et al., 2012). If habitat quality is dynamic (e.g., due to wind variability) then I would expect female distribution and movement among spawning sites to reflect these changes. Males should employ strategies to remain on the breeding areas throughout the spawning season to increase reproductive success (de Gaudemar, 1998; Muir et al., 2012). Thus, I expect male distribution to reflect that of females to maximize reproductive success. Most studies to date have investigated lake trout mating systems only at small spawning site scales and have yet to characterize male and female behaviour at a whole lake scale (Muir et al., 2012). Although some researchers have observed lake trout movements during the spawn (Eschmeyer, 1955; MacLean et al., 1981; Martin, 1957), the reproductive strategies for male and female lake trout are still largely unknown. Further, sexual selection in terms of mate choice and competition is virtually unknown for lake trout, but important to achieve a more comprehensive understanding of lake trout reproductive strategies (Esteve et al., 2008).

1.4 Northern development

Development and mining in Canada's North are expected to increase in the near future (Rhéaume and Caron-Vuotari, 2013). Many of these operations will impact the lakes and waterways that define northern Canada (Cott et al. 2015a). Currently there exists little information detailing the reproductive behaviour of lake trout in northern lakes, so it is assumed that observations of lake trout reproduction from the southern extent of their range are similar to northern locales. Because of large climatic differences between southern and northern regions, the use of southern-derived data can be misleading. Northern-specific data on spawning habitat characteristics and use is not only imperative to the sustainability of northern lake trout, but also for taking a proactive and adaptive approach to managing northern fisheries in the future.

1.5 Objectives

My Master's thesis will investigate lake trout reproduction in a northern lake. I focus on (1) lake trout spawning habitat and correlates of embryonic survival, and (2) reproductive strategies between males and females. For the first objective, I investigate whether northern lake trout spawn on areas of high wind exposure with clean substrate, similar to southern observations, and test if lake trout embryonic survival is positively related to wind exposure. For the second objective, I determine when and where lake trout spawn in a typical northern boreal lake. I also describe sex-specific timing and movements of lake trout over the duration of a spawning season and explore what reproductive strategies male and female employ during the spawning season. Specifically, I test if male and female lake trout spawn at more than one site as a bet-

hedging strategy. My thesis not only characterizes critical lake trout spawning habitat in northern lakes, as well as provide a detailed assessment of the lake trout mating system, it acts as a platform for future research of economically, recreationally and culturally important fish species to ensure we conserve and sustain northern fisheries and fish species diversity.

Chapter 2: Lake trout (*Salvelinus namaycush*) spawning habitat in a northern lake: the role of wind and physical characteristics on habitat quality*

David T. Callaghan^{1*}, Paul J. Blanchfield^{1,2}, and Peter A. Cott³

¹ Department of Biological Sciences, University of Manitoba, 50 Sifton Road, Winnipeg, MB R3T 2N2, Canada

² Freshwater Institute, Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, MB, R3T 2N6, Canada

³ Cumulative Impact Monitoring Program - Environment and Natural Resources, Government of the Northwest Territories, Box 1320, Yellowknife, Northwest Territories X1A 2L9, Canada.

* Reprinted from Callaghan, D.T., Blanchfield, P.J., and Cott, P.A., (2015) Lake trout (*Salvelinus namaycush*) spawning habitat in a northern lake: The role of wind and physical characteristics on habitat quality. *Journal of Great Lakes Research*.

2.1 Introduction

The distribution of native lake trout (*Salvelinus namaycush*) populations is confined to the northern portions of North America (Martin and Olver, 1980). This species is well adapted to the demanding and dynamic conditions of the Arctic and Boreal regions of Canada, and is found across the Precambrian Shield (Gunn et al., 2004). Throughout its range, lake trout are of commercial, recreational and aboriginal importance. There are an estimated 87,125 lake trout lakes in Canada, 28 % of which occur in the Northwest Territories (NWT) and Yukon (Sharma et al., 2009). Despite an extensive northern distribution (Sawatzky et al., 2007), most studies on lake trout are from the southern extent of their range, and almost absent from northern boreal lakes. Importantly, critical habitat parameters for the maintenance of lake trout populations, such as spawning habitat quality and its relationship to embryonic survival, are still largely unknown for northern regions (Muir et al., 2012). Our limited understanding of lake trout ecology in the core of the species' range represents a concerning knowledge gap, especially as climate is predicted to rapidly change at high latitudes (Quesada et al., 2006), and industrial activity in Canada's North is expected to increase in the near future (Rhéaume and Caron-Vuotari, 2013), and can impact fish and fish habitat (Cott et al., 2015a).

Lake trout are a long-lived species that exhibit iteroparous spawning. In autumn, lake trout migrate onto shoals in nearshore areas of lakes (Gunn, 1995); the timing generally coincides with surface water temperatures declining to 12 °C or lower (Redick, 1967). Eggs are spawned directly onto substrate, and, unlike all other salmonine species, no parental care is provided (i.e., no redd is constructed by the female). Eggs fall into the

interstices of the cobble substrate and remain there for several months before emerging (Royce, 1951). Therefore, an essential behavioural trait of lake trout is the ability to select high quality spawning habitat to ensure embryonic survival (Gunn, 1995; Muir et al., 2012). Spawning site selection may even be more critical in high latitude lakes, where lake trout are known to skip spawning in some years to conserve energy (Miller and Kennedy, 1948).

A general feature of lake trout spawning habitat is well-sorted cobble substrate with interstitial areas large enough for lake trout egg incubation. This habitat is predominately found near exposed shorelines off of points, islands or on mid-lake shoals (Martin and Olver, 1980), and some glacial bedforms such as drumlins (Riley et al., 2014). Most spawning shoals are less than 6 m deep (Martin and Olver, 1980) and situated close to deep water (Royce, 1951), but can range from very shallow in small lakes (0.15 m in Squam Lake, New Hampshire; Merriman, 1935) to 40 – 50 m in the Laurentian Great Lakes (Janssen et al., 2006), with evidence of potential spawning at >91 m depth in Lake Superior (Eschmeyer, 1964). Lake trout spawning areas are usually composed of clean pebble and cobble, broken rubble, or angular rock (mainly 3–15 cm in diameter) along with dispersed boulders (Martin and Olver, 1980). Substrate size appears to be a critical feature of lake trout spawning shoals (Sly, 1988). For example, experimental covering of traditional spawning shoals in a small boreal lake resulted in lake trout spawning on alternate sites with similar substrate size (McAughey and Gunn, 1995). Presumably, substrate size is important to developing embryos for both oxygen-exchange and exclusion of egg predators (Gunn, 1995).

In addition to physical habitat features, wind events appear to play an important role in lake trout reproduction (Muir et al., 2012). There is substantive evidence linking lake trout migration onto spawning shoals with strong autumn winds (Deroche, 1969; Esteve et al., 2008; Martin, 1957; Muir et al., 2012; Royce, 1951). Further, lake trout spawning shoals typically face prevailing winds, suggesting that wind plays a definitive role in habitat quality. Currents induced by wind can be beneficial to egg incubation by removing fine sediments from the interstitial areas where eggs are deposited while circulating oxygenated water (Gunn, 1995; Sly, 1988). However, there is also evidence that high wave exposure and large wind fetch, such as on lake trout spawning shoals in the Laurentian Great Lakes, can result in lower embryonic survival (Eshenroder et al., 1995; Fitzsimons, 1995; Manny et al., 1995; Perkins and Krueger, 1995). Thus, the extent to which wind influences lake trout embryonic survival is not fully understood. Due to the dynamic nature of wind, wind-influenced habitat quality vary spatially and temporally throughout the course of a spawning season, as well as among years.

Because much of what we know about lake trout spawning has been derived from southern regions, an initial goal of this study is to characterize lake trout spawning habitat in a typical northern boreal lake. We focus on two key features of lake trout spawning shoals – substrate size and wind exposure – to address the hypothesis that lake trout spawning habitat in a northern lake is similar to that reported for the southern periphery of their range. Specifically, we investigate whether northern lake trout spawn on areas of high wind exposure with clean substrate. A second aim of this study is to quantify abiotic correlates of lake trout embryonic survival within a northern lake. We predicted that lake trout embryonic survival would be positively related to wind exposure. Therefore, we

developed a wind exposure model to examine embryonic survival in incubators placed on various spawning shoals that experience a gradient in wind and wave exposure. Gaining information on spawning habitats of northern lake trout will be useful for researchers and resource managers dealing with the cumulative effects of multiple stressors on northern aquatic systems ranging from increased industrial development to an unpredictably changing climate.

2.2 Methods

2.2.1 Study site

Our study was conducted in, Alexie Lake (62° 40' N, 114° 05' W), located in south-central NWT, Canada, approximately 30 km northeast of Yellowknife, at the Chitty Lakes Research Reserve (Fig. 2.1). Alexie Lake is a medium-sized oligotrophic lake covering an area of 402 ha (Guzzo et al., 2015), possessing 35 islands and a shoreline length of 28 km. Maximum depth in Alexie lake is 32 m with a mean depth of 11.7 m. Stratification occurs during the summer until September when the lake becomes isothermal (Healey and Woodall, 1973). Alexie Lake is in the core of this species range and the size, physical, and limnological characteristics make it a “typical” lake trout lake (Gunn et al., 2004). In addition to lake trout, Alexie Lake contains two other piscivorous species, burbot (*Lota lota*), northern pike (*Esox lucius*), as well as numerous prey fish species (see Cott et al., 2011), including sculpins, *Cottus sp.* and lake whitefish (*Coregonus clupeaformis*), all known lake trout egg predators. Alexie Lake is a designated research lake that is closed to fishing.

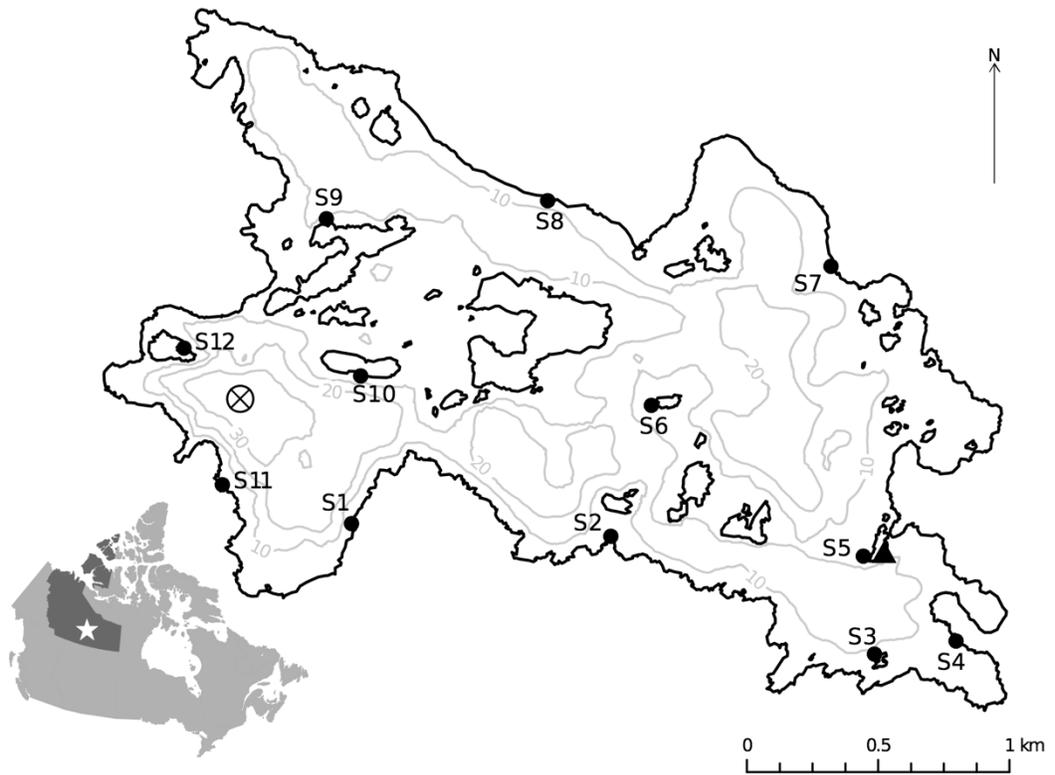


Figure 2.1 – The locations of 12 spawning sites (S1-S12) sampled in Alexie Lake, NWT. The bathymetric contours (grey lines) are at 10 m increments. The locations of the temperature logger string (circle containing an x) and weather station (triangle) are indicated.

2.2.2 *Spawning habitat*

We attempted to determine where lake trout spawning occurred in Alexie Lake based on direct observation (P. Cott and M. Guzzo, personal communication, 2013), and telemetry data collected during the 2012 spawning season (Guzzo et al., in press). In the spring of 2013, we conducted boat and snorkel surveys of much of the shoreline of Alexie Lake, and selected 11 sites (S1–S11) we believed to be possible lake trout spawning shoals based on the general physical habitat characteristic of clean pebble and cobble substrate, and the information from previous seasons. The selected sites were distributed around Alexie Lake (Fig. 2.1), and therefore were predicted to receive a gradient of wind exposure during the 2013 spawning season. An additional site was designated for reference (S12; Fig. 2.1). This reference site, sheltered from most wind directions, had otherwise similar substrate, depth and slope as the other wind-exposed sites, however lake trout telemetry data showed limited activity in the immediate area. In Alexie Lake, lake trout spawning is known to start in early September and last several weeks (P. Cott, unpublished data). We conducted snorkel surveys at each of the 12 sites every other day for the month of September 2013 to confirm whether spawning occurred at these locations.

Data on physical habitat characteristics including; shoal depth, slope, interstitial depth, and substrate length, width and shape, were collected from three locations on each spawning shoal site. These shoals were selected after spawning was confirmed during snorkel surveys in the fall of 2013. These physical measurements of the spawning shoals were conducted the following spring (June 2014), so as to not disturb lake trout spawning. A sampling hoop (70 cm diam.) was placed on the spawning shoal by

snorkelers and the shoal depth was measured from the water surface to the substrate at the centre of the sampling hoop. Slope (%) was calculated as:

$$Slope = \frac{rise}{run} \times 100\% \quad (1)$$

Where rise is the difference between measured drop off depth, or the edge of where the depositional zone (silt and sand) meets the erosive zone (boulders, rocks, cobble, and pebble) and measured shoal depth, and run is the measured distance from the centre of the sampling hoop to the end of the drop off. Substrate within the sampling hoop was evenly collected from the surface of the shoal and placed into a bucket. A random sample of substrate ($n = 20$ pieces) was measured for length and width, defined as the longest axis and second longest axis, respectively. An index for two-dimensional morphologic shape (elongation) was used to calculate substrate shape by dividing width by length (Blott and Pye, 2008). Elongation values closer to 0 indicate greater elongation, while values closer to 1 indicate greater roundness. Interstitial depth was measured by first excavating a pit within the sampling hoop and inserting a rigid ruler vertically to a maximum depth of 25 cm or until sand, silt or bedrock was reached. Interstitial depths that exceeded 25 cm were assigned a value of >25 cm.

2.2.3 Wind data collection and wind exposure modelling

We installed a meteorological station (HOBO® micro station data logger: model H21-002, Onset® Computer Corporation, Cape Cod, MA) with an attached anemometer (R.M. Young wind monitor: model 05103, R.M. Young Company, Traverse City, MI) to record wind direction ($\pm 3^\circ$) and speed ($\pm 0.3 \text{ m s}^{-1}$) at 5 m elevation above lake level on an island in the southeast region of Alexie Lake (Fig. 2.1). Mean half-hourly wind

velocity and wind direction data were collected for a period of 2 years (September 19, 2012 to September 29, 2014), which encompassed three consecutive lake trout spawning seasons (roughly defined as the month of September). Mean wind direction was calculated using the following equations (Hafner and Hites, 2005):

$$X = \left(\frac{1}{n}\right) \sum_{i=1}^n \cos \theta_i \quad (2)$$

$$Y = \left(\frac{1}{n}\right) \sum_{i=1}^n \sin \theta_i \quad (3)$$

$$\theta = \frac{180}{\pi} \arctan\left(\frac{Y}{X}\right) \quad (4)$$

where θ_i is the half-hourly wind direction angle (in radians), n is the number of observations, θ is the average angle (in degrees). Wind direction (θ) ranged from -180° to 180° , where 0° corresponds to north and $\pm 180^\circ$ corresponds to south. Wind direction was converted to the commonly used compass direction by adding 360° to all negative θ values. To assess the variability of the average wind direction, angular deviation, s , was calculated using (Hafner and Hites, 2005):

$$d = \sqrt{X^2 + Y^2} \quad (5)$$

$$s = \frac{180}{\pi} \sqrt{-2 \ln d} \quad (6)$$

To determine annual variability in persistence of wind speeds, we developed cumulative wind speed duration curves for each of the three spawning seasons, 2012, 2013, and 2014. For modelling purposes a spawning season was defined as the month of September. The wind speed duration curve represents the percentage of time that each

wind measurement equals or exceeds a particular value (Koçak, 2008). Specifically, we were interested in comparing annual differences in the presence of wind speeds that were $\geq 3.3 \text{ m s}^{-1}$ (11.9 km h⁻¹); the speed we estimated to promote currents at lake trout spawning shoals (see below).

A wind-based linear fetch model was developed to estimate wind speeds that would produce waves capable of inducing sediment resuspension through near-bottom currents at Alexie Lake spawning shoal depths (~2 m). Near-bottom current velocities $u_{\text{max}} \geq 0.1 \text{ m s}^{-1}$ are known to cause sediment resuspension in nearshore zones (Seibt et al., 2013). Near-bottom current velocity was calculated by determining maximum orbital velocity (u_{max}):

$$u_{\text{max}} = \frac{\omega H_{\text{sig}}}{2 \sinh\left(\frac{\pi d}{L}\right)} \quad (7)$$

where ω is angular velocity, H_{sig} is significant wave height, d is water depth, and L is wavelength (see Hallermeier 1981). A series of incremental wind speeds (+0.1 m s⁻¹) were added to the model until a maximum u_{max} value of at least 0.1 m s⁻¹ was achieved in the nearshore regions for all 8 primary fetch directions (north, northeast, east, southeast, south, southwest, west, and northwest). It was determined that wind speeds of 3.3 m s⁻¹ or greater were required to induce a $u_{\text{max}} \geq 0.1 \text{ m s}^{-1}$ in the nearshore regions of Alexie Lake.

Using detailed bathymetric data, including depth, slope, fetch length, and local wind data, we produced another wind-based linear fetch model to predict the location of erosive zones, where fine-grain sediment do not accumulate due to wind exposure.

Erosive zones are determined by calculating the mud deposition boundary depth (mud DBD):

$$\log DBD = -0.107 + 0.743 \log F + 0.0653S \quad (8)$$

where F is fetch (km), and S is slope (%) (Rowan et al., 1992). Locations where actual depth equaled the predicted mud DBD are defined as the boundary of the erosive zone. Areas within 1 m depth of the estimated mud DBD are considered the transition zone between erosive and depositional zones of the lake (*sensu* Flavelle et al., 2002). The erosive transition zone is assigned a value (between 0 and 1) based on proportion of wind exposure produced by wind speeds $\geq 3.3 \text{ m s}^{-1}$ throughout the lake trout spawning season. We used the output of this model to quantify wind exposure across the 12 study sites in Alexie Lake, and to compare to embryonic survival (see below).

2.2.4 Embryonic survival

We conducted an experiment to determine how wind exposure (based on the results of the wind exposure model) influences lake trout embryonic survival. Three ripe females were captured by angling on September 25, 2013. Eggs collected from each female were kept separate and fertilized using the combined milt from two males that were previously captured and held in a pen. To ensure viable eggs were used in the incubation experiment, eggs were allowed to water harden overnight and fertilization was verified prior to loading into Jordan/Scotty® incubators. Each incubator received 50 fertilized eggs from each female (150 total), which were kept separate within a single incubator. Incubators were deployed at each of the 12 sites on September 26, 2013, and retrieved through the ice January 8–10, 2014, prior to the expected hatching date,

allowing for 102–104 days of in situ incubation. Small holes (5 mm diam.) at the bottom and top of each incubator cell allowed for water circulation through the incubator (similar to interstitial areas in cobble substrate), but protected eggs within from most egg predators. Once retrieved, incubators were placed in a cooler of lake water and brought back to the Chitty Lake Research Station for visual examination. Each incubator cell was classified as alive, dead, or empty. Proportion survived was calculated for each female as number of live eggs divided by total cells (50). Eggs were preserved in a 10% formalin solution. Empty cells were assumed to be dead eggs. This assumption was tested by modelling egg development based on Allen et al. (2005) zero hatch model:

$$D = a \left(\frac{T}{b - T} \right)^c \quad (9)$$

where D represents developmental rate of lake trout eggs, T is temperature in degrees Celsius, and a , b , and c are constants. Expected hatching date and 95% confidence interval (95% CI) were predicted by bootstrapping the distribution of parameter estimates published by Allen et al. (2005) and temperature at 2 m depth during incubation 10,000 times. The zero hatch model was developed with lake trout embryos from the Marquette brood stock (Allen et al., 2005), which may develop at a different rate than those from Alexie Lake. Horns (1985) has shown that different lake trout stocks may hatch as much as 18 days apart under the same incubation conditions. We felt that including 95% confidence intervals for predicted hatch day estimates would help encompass possible lake trout development variation in Alexie Lake. Water temperature in Alexie Lake was recorded on HOBO® Pendant™ temperature loggers (Onset® Computer Corporation, Borne, MA) at 1 m intervals through the water column in the

deepest basin. Although lake trout embryos were placed in incubators and not in direct contact with the shoal, characteristics such as substrate length and shape, as well as slope and depth, likely influence site-specific interstitial flow, and therefore we assumed these features could influence embryonic survival in the incubation trays.

2.2.5 Statistical analysis

Differences in shoal slopes among spawning sites was tested using an ANOVA. Substrate length was cube root transformed to meet normality assumptions, although variances remained heterogeneous; differences among sites were tested using a Welch's ANOVA for unequal variances. An ANOVA was used to test for differences in wind exposure across sites and among years. Substrate shape as well as wind speed data did not meet parametric assumptions, and differences among sites were tested using a Kruskal-Wallis rank sum test. The distributions of wind directions among years were compared using a non-parametric Mardia-Watson-Wheeler test for circular data. Female effect on embryonic survival, and differences in embryonic survival among sites, were tested using a non-parametric Kruskal-Wallis test. We tested predictors of lake trout habitat quality and its effect on embryonic survival using a generalized linear model (GLM) with quasibinomial error structure after determining our data were underdispersed; $\phi = 0.49$ (Zuur et al., 2009). Predictors were selected based on common measurements of spawning habitat quality (Marsden et al., 1995). We sequentially culled parameters from the global model: Embryonic survival = Wind Exposure + Shoal Depth + Slope + Substrate Length + Substrate Shape, to obtain all possible combinations of predictor parameters. We then determined the best model, using weight ratios derived

from quasi-likelihood Akaike Information Criterion (QAICc) adjusted for underdispersion.

2.3 Results

2.3.1 Spawning habitat

We observed male and female lake trout at each of the 11 locations that we had selected as potential spawning sites during snorkel surveys throughout the month of September in 2013. In addition, we either observed lake trout spawning behaviour or the presence of lake trout eggs at all 11 sites. We also found evidence of spawning (lake trout eggs present) at S12, which was originally designated as a non-spawning shoal reference site, and therefore this site was included as an additional spawning site (Fig. 2.1).

All lake trout spawning sites found in Alexie Lake were easily identifiable with a clean cobble strip at the offshore edge of the shoal, where a boulder wall (rock crib) appeared to act as a barrier, holding back the pebble and cobble as well as sand and silt backfill (Fig. 2.2). The rock crib rose abruptly from the lake bottom at depths of 128–438 cm (mean \pm SD: 292.7 \pm 81 cm) in the nearshore regions of Alexie Lake, forming an obvious vertical wall (Fig. 2.2). Spawning shoal water depth ranged between 89 cm and 178 cm (134.4 \pm 20.7 cm). The slope of the rock crib did not differ significantly among sites (ANOVA: $F_{(11,24)} = 1.73$, $p = 0.13$), and ranged from 12% to 63% with a mean slope of 42 \pm 13%.

Lake trout spawning substrate was predominately comprised of rounded granite pebble and cobble of variable length that ranged in size from 1.3 cm to 21.7 cm (8.9 \pm 3.8 cm, Fig. 2.3a). Most spawning substrate (92%) was between 3–15 cm; a size range that is

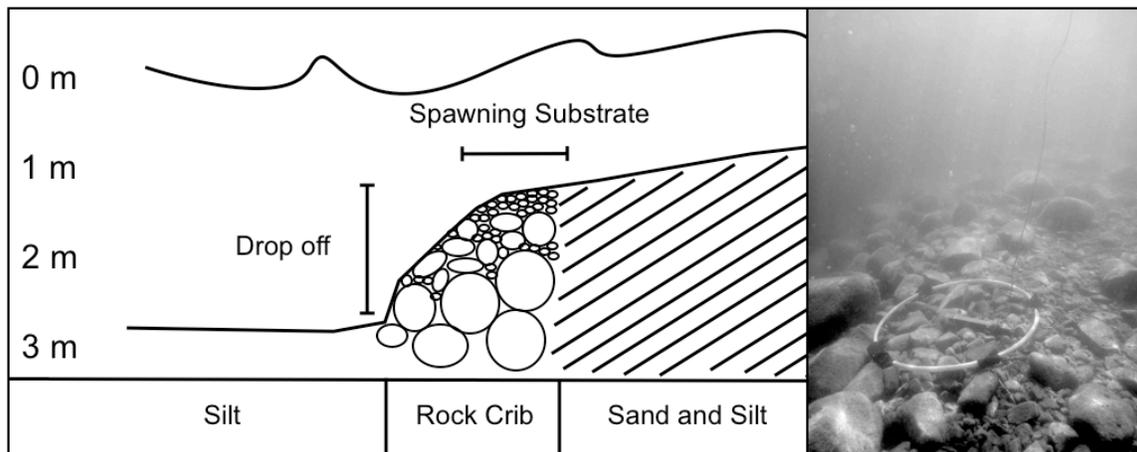


Figure 2.2 – Profile of a typical Alexie Lake, NWT, spawning shoal (left). Three zones are depicted from offshore to nearshore: the silt zone located offshore before the drop-off; the rock crib located at the drop off where spawning occurs; and the sand and silt zone towards the shoreline. A photograph depicts a sampling hoop and ruler during habitat sampling on a typical spawning shoal in Alexie Lake.

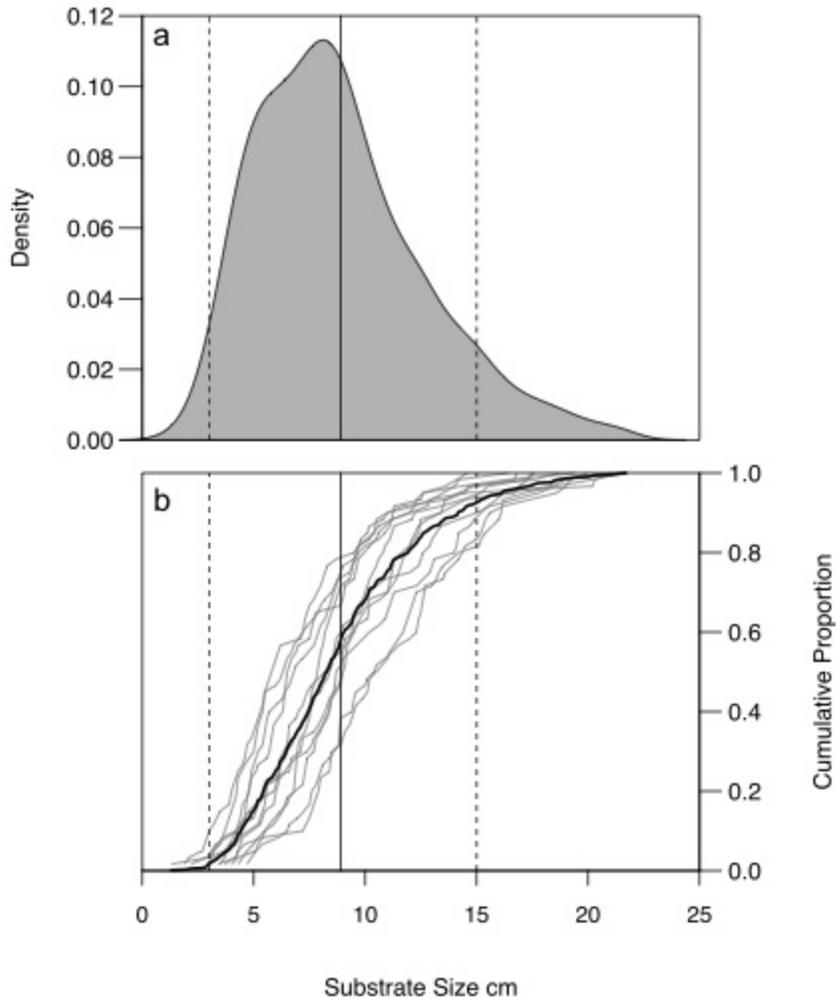


Figure 2.3 – a) Kernel density estimate of substrate size for selected lake trout spawning sites in Alexie Lake, NWT (see Fig. 1), and (b) cumulative proportion distributions of substrate size for each spawning site. Dashed lines represent the minimum (3 cm) and maximum (15 cm) spawning substrate size used by lake trout (Martin and Olver, 1980). The solid line represents the mean (8.9 cm) substrate size in Alexie Lake.

considered typical for the species (Martin and Olver, 1980). Despite a typical lake-wide size distribution of spawning substrate, we observed significant variation in substrate characteristics among the 12 study sites (Fig. 2.3b). For example, individual spawning sites ranged from those predominantly comprised of large cobble (68% of which was > the mean 8.9 cm), to sites that included mainly small cobble and pebble (78% \leq 8.9 cm). Small cobble and pebble (\leq 8.9 cm) was the most commonly occurring substrate on the spawning shoals and comprised >50% of the substrate distribution for two-thirds ($n = 8$) of lake trout spawning shoals studied in Alexie Lake. Mean substrate length was significantly different among sites (Welch's ANOVA: $F_{(11,278.58)} = 9.42$, $p < 0.001$). Mean shape of the cobble varied among sites, but was generally found to be more rounded than elongate (i.e. closer to 1; overall mean shape: 0.70 ± 0.17). Significant differences in mean shape were found among sites (Kruskal-Wallis: $H = 26.83$, $N = 12$, $p = 0.005$). Interstitial depths were usually >25 cm (61% of sampled sites; $n = 36$), with at least one sample location >25 cm in depth at each of the 12 sites. A minimum interstitial depth of 12 cm was observed at one site. All interstitial areas were absent of fine sediment (silt or sand) or algae.

2.3.2 Wind

Wind direction and intensity during the period of lake trout spawning at Alexie Lake varied within and among years (Fig. 2.4). Mean wind direction in 2012 was from the west at a compass bearing of $277 \pm 74^\circ$ (mean \pm angular deviation), while in 2013 and 2014, mean wind direction was from the southwest ($238 \pm 80^\circ$ and $231 \pm 98^\circ$, respectively). The distribution of wind directions differed significantly between each spawning season (Mardia-Watson-Wheeler : 2012 and 2013, $W = 79.08$, $p < 0.001$; 2012

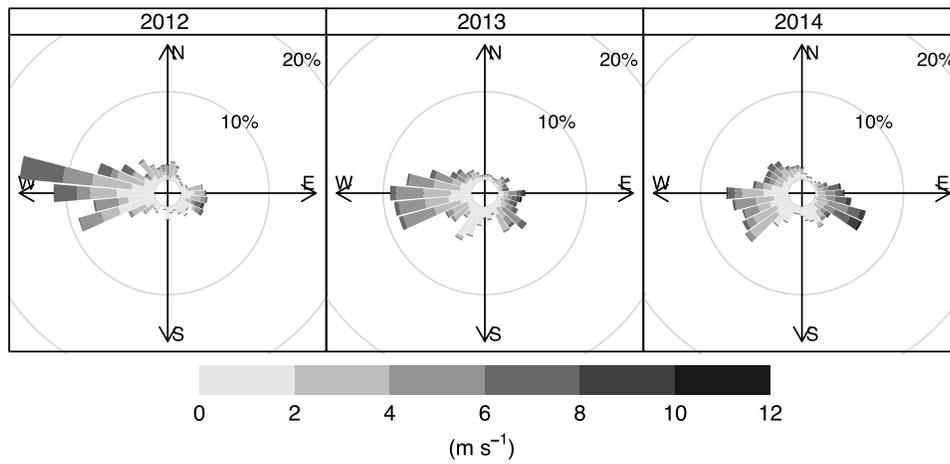


Figure 2.4 –Relative frequency of wind direction and related wind speed prevailing during three consecutive lake trout spawning seasons (September 19 to October 1, 2012; September 1 to October 1, 2013; September 1 to 29, 2014) at Alexie Lake, NWT, are expressed as wind roses. Radii represent 10-degree bins.

and 2014, $W = 112.09$, $p < 0.001$; 2013 and 2014, $W = 29.13$, $p < 0.001$). Wind direction frequency varied little between the 2012 and 2013 spawning seasons; 45% and 36% of wind originated from the west in these years, respectively. Wind direction was more variable during the 2014 spawning season, in which 23% was from the west, 19% from the southwest, 17% from the east, and 15% from the southeast (Fig. 2.4). Although wind predominantly came from the west, the strongest winds came largely from the east and southeast. All (100%) strong winds ($>8 \text{ m s}^{-1}$) in 2012, and most (91%) in 2013 were from the east, with a maximum sustained gust speed of 14.0 m s^{-1} and 16.2 m s^{-1} , respectively. In 2014 the wind was more variable, but wind speeds $>8 \text{ m s}^{-1}$ were predominately from the east (44%) and southeast (45%), with maximum sustained wind gusts of 15.2 m s^{-1} for both directions.

Mean wind speed during 2012 ($2.90 \pm 2.06 \text{ m s}^{-1}$) was significantly lower than 2013 and 2014 ($3.26 \pm 2.05 \text{ m s}^{-1}$, $3.33 \pm 2.36 \text{ m s}^{-1}$, respectively; $H = 14.09$, $N = 3$, $p < 0.001$). Despite the observed differences in wind direction and speed among spawning seasons at Alexie Lake, we measured similar levels of high wind intensity, believed to be important for lake trout reproduction, across all years. Specifically, winds $\geq 3.3 \text{ m s}^{-1}$, which are predicted to induce near-bottom water currents at spawning shoal depths of $\sim 2 \text{ m}$, comprised 43%, 42%, and 36% of all winds during the month of September in 2012, 2013, and 2014, respectively.

2.3.3 Wind exposure model

Modelled wind exposure (the proportion of wind speeds $\geq 3.3 \text{ m s}^{-1}$), varied significantly among lake trout spawning sites in Alexie Lake ($F_{(11,22)} = 10.18$, $p < 0.001$),

as well as among years ($F_{(2,22)} = 13.03, p < 0.001$). Mean wind exposure for sites located on the west side of Alexie Lake (S11 and S12, Fig. 2.5) was significantly lower than all other spawning sites in each of the three years. Further, proportion of wind exposure at these western spawning sites was always <0.4 ; while sites S1–S10 always had wind exposure >0.4 . Site S9 consistently experienced the highest proportion of wind exposure each year, always exceeding 0.7. Wind exposure in 2012 was significantly higher among sites than in 2013 and 2014; no difference was found between 2013 and 2014. In 2012, six sites had wind exposure proportions >0.7 , while in subsequent years (2013 and 2014) only one site had a proportion of wind exposure >0.7 .

2.3.4 Embryonic survival

We estimated that mean hatch date of lake trout embryos from the deployment date of egg incubators in Alexie Lake was 130 d (95% CI; 99 d, 168 d), equivalent to February 3, 2014 (95% CI; January 3, 2014, March 13, 2014). Although our collection dates (January 8–10, 2014) fell within the upper 95% CI, we found no signs of hatching or failed escapes from examination of embryos, and assume empty cells, as a result of hatching, to be highly unlikely.

Embryonic survival did not vary among females ($H = 3.25, N = 3, p = 0.16$), but did vary among sites ($H = 26.763, N = 12, p = 0.005$; Fig. 2.6). Mean embryonic survival among sites in Alexie Lake was 47%, but ranged from 2% to 83%. Survival exceeded 80% at three sites (Fig. 2.6). The mean proportion of wind exposure for all sites during incubation, defined as the period from the day after deployment until surface ice formation (September 27 – November 9, 2013), was 0.55 and ranged from 0.29 to 0.84.

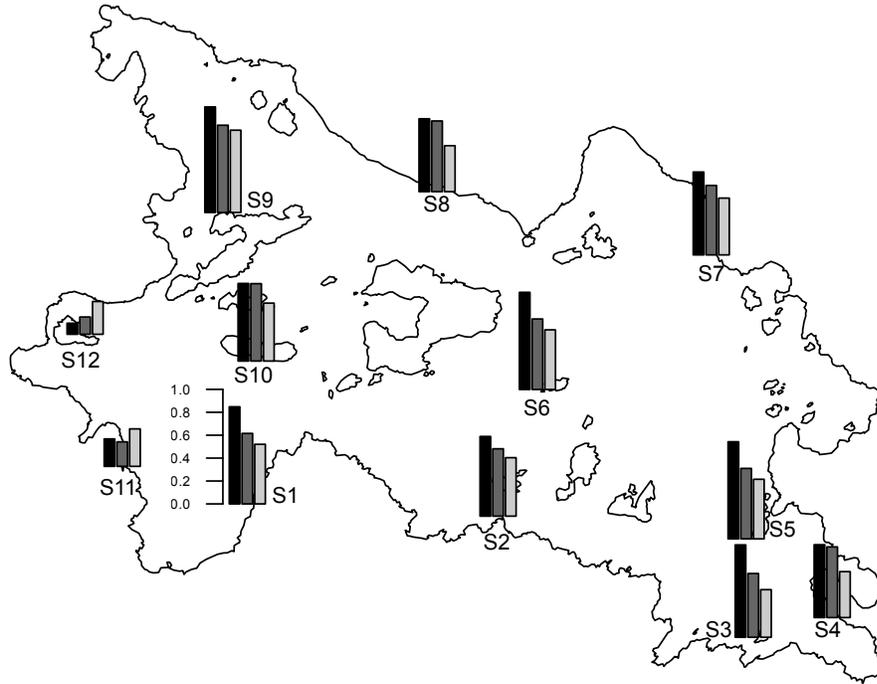


Figure 2.5 – Modelled estimates of wind exposure at 12 lake trout spawning sites in Alexie Lake, NWT (see Fig. 1). Bars represent the proportion of wind speeds that result in water currents (i.e. $\geq 3.3 \text{ m s}^{-1}$) at each site during three consecutive spawning seasons (2012 black; 2013 dark grey; 2014 light grey).

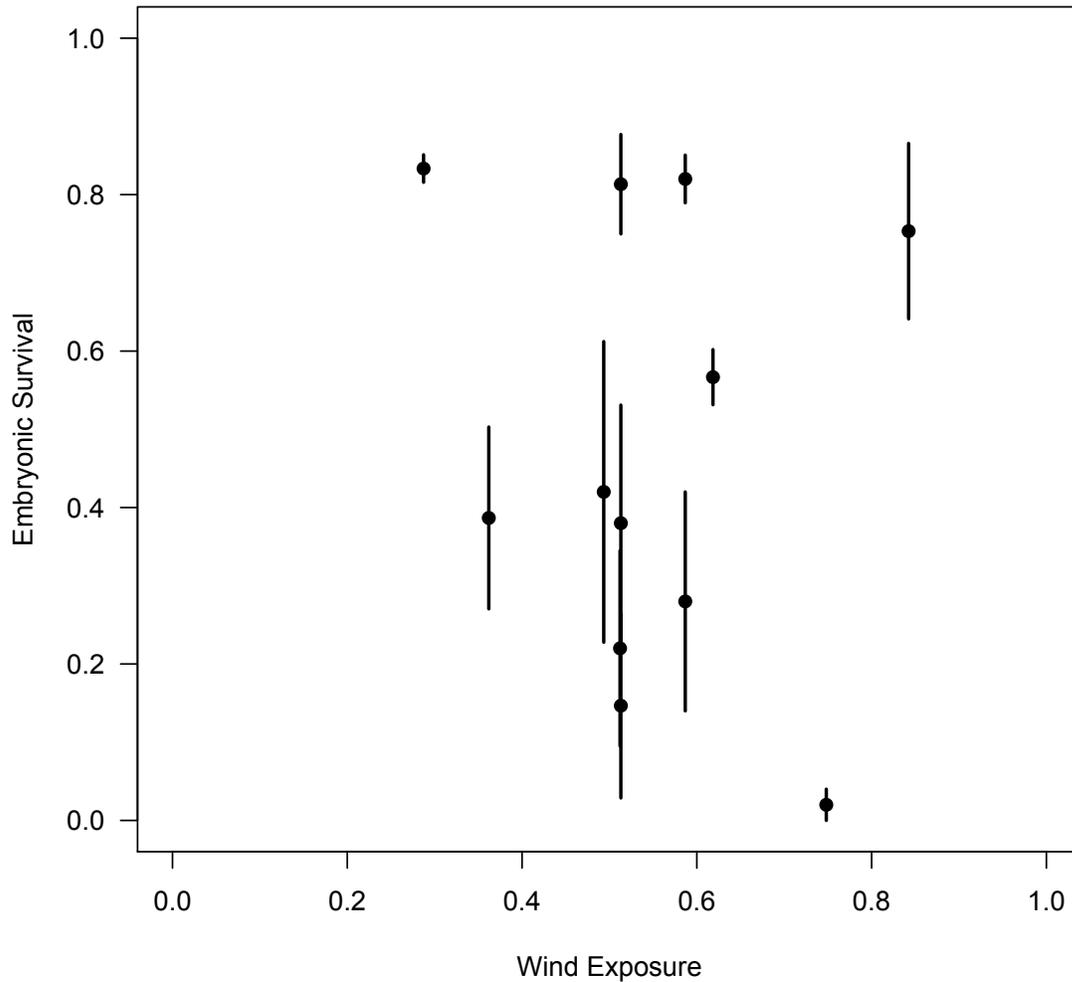


Figure 2.6 – The relationship between wind exposure (wind speeds $\geq 3.3 \text{ m s}^{-1}$) during the open water period (September 27–November 10, 2013) and embryonic survival for lake trout eggs held in incubation trays until January 8–10, 2014 in Alexie Lake, NWT.

Embryonic survival is the mean proportion (\pm SEM) of eggs from three females at each

spawning site (see Fig. 1) determined to be alive in relation to proportion of wind exposure.

Only two sites had wind exposure >0.7 , of which S2 had a mean embryonic survival of 2%, and S9 had much higher survival (75%). The quasibinomial GLM showed that wind exposure had no effect on embryonic survival (Table 2.1). Furthermore, none of the physical habitat features of spawning sites including depth, slope, substrate length, substrate shape were found to be significant factors influencing embryonic survival (Table 2.1). This result was further supported by QAICc model selection, which indicated that the null model best described embryonic survival. Ice depth for each site at the time of incubator collection ranged from 49 cm to 75 cm, with a mean of 60.1 ± 6.8 cm.

2.4 Discussion

Lake trout spawning habitat has long been characterized as wave-swept cobble shoals that face predominant autumn wind directions; we found only partial support for this characterization in a northern lake. We observed high variability in wind direction and intensity within and among spawning seasons in Alexie Lake. Wind was predominately from the west during the three spawning seasons, but high intensity winds ($>8 \text{ m s}^{-1}$) largely came from the east and southeast. Despite the variability in wind direction, the proportions of wind speeds predicted to induce near-bottom currents ($\geq 3.3 \text{ m s}^{-1}$) were similar among years (36–43%). Wind exposure was least variable in 2012, and appeared to be a result of the dominant west wind in this year. Overall greater wind exposure during 2012 is attributed to the orientation of most sites to receive westerly winds. In years with greater variability in wind direction (2013 and 2014), wind exposure

over all sites was reduced. High variability in wind direction within and across spawning seasons suggests that predominant wind is not a predictable feature of lake trout spawning habitat selection in this northern lake. Further, changing climate may lead to

***Table 2.1** – Parameter estimates of quasibinomial generalized linear model on the global model for predicting embryonic survival. The explanatory variables included wind exposure (wind), spawning shoal slope (slope), depth of embryo incubator (depth), mean length of substrate (length), and mean shape of substrate (shape). Residual deviance: 2.81 on 6 degrees of freedom. QAICc ranked the null model (intercept only) as the top model describing embryonic survival.*

	Estimate	Std. Error	t value	<i>p</i>
Intercept	-0.55	8.57	-0.06	0.95
Wind	1.48	3.94	0.37	0.72
Slope	-0.05	0.05	-0.98	0.37
Depth	-0.02	0.03	-0.46	0.66
Length	0.04	0.25	0.16	0.88
Shape	4.73	10.18	0.46	0.66

greater variability in wind direction and speed. Notably, northwestern Canada (Yukon and Northwest Territories) has experienced declining wind speeds over the last half century (1953-2006; Wan et al., 2010), which, if this trend continues, may result in weaker and less reliable autumn winds in the future.

Suitable lake trout spawning substrate in Alexie Lake was widespread (virtually around the entire lake), while wind direction was found to be unpredictable within and among spawning seasons. Based on data from the local meteorological station at Alexie Lake showing predominant wind direction originating from the west in 2012, we predicted that the primary location of spawning shoals would be along eastern shorelines (including islands). This was not the case, as we found lake trout spawning to be widespread, occurring at all sites (Fig. 2.1). In fact, despite limited exposure to winds that were of sufficient strength to result in interstitial water movement (based on modelling), lake trout were observed to spawn on westerly sites, including wind-sheltered locations. Variation of wind direction in conjunction with abundance of suitable spawning substrate likely contributed to the widespread distribution of spawning shoals in Alexie Lake and may be a common feature for northern lakes with limited fetch.

Spawning habitat in Alexie Lake was easily identifiable, with a characteristic clean substrate strip along the leading edge of a boulder drop-off slope (rock crib) that formed an abrupt step from the lake bed to the top of the shoal (Fig. 2.2). Lake trout spawning sites in this northern lake were of similar depths (<2 m) to those found in small southern lakes (Gunn, 1995). The depth at which spawning occurs is presumably of great importance. First, spawning shoals must be shallow enough for wind-generated currents to reach the substrate and penetrate the interstices to keep these areas free of silt. Second,

the shoals must be deep enough to avoid freezing and ice scour during incubation (Claramunt et al., 2005). Likewise, slope also appears to be an important feature of lake trout spawning habitat by aiding in the formation of interstitial water currents. In Alexie Lake, shoals generally appear as a distinct step rising 1 to 3 m from the gradual lake bed at the base of the rock crib to the top of the spawning shoal with a slope of 42% or 23°. Riley et al. (2014) describe a similar habitat in the Laurentian Great Lakes, where drumlins rise from the lake bed and intercept currents. The interaction of glacial bedforms with currents is hypothesized to generate interstitial flow via the Bernoulli Effect, whereby an abrupt change in depth accelerates current flow and lowers pressure downstream, which forces water through interstitial areas of spawning substrate and prevents settling of small particles. This interstitial flow likely also occurs in Alexie Lake where very clean substrate was found at the leading edge of an abrupt step. Habitat features that allow interstitial water movement appear to be a critical factor for lake trout embryo incubation, and one that can take a variety of forms: ‘classic’ wave-swept shoals (Martin, 1957; Royce, 1951); drumlins in Lake Huron (Riley et al., 2014); or rock cribs (this study). Similar spawning habitat to Alexie Lake was also found in an adjacent lake (Chitty Lake), with lake trout eggs present (personal observation). The spawning habitat described in this study – a clean pebble and cobble strip at the leading edge of a rock crib – may be a widespread habitat feature for lake trout reproduction in northern lakes.

A common requirement of all salmonines is interstitial flow during the egg incubation period (Chapman, 1988). In rivers and streams, the downstream flow of water achieves this; conversely, in lakes, water currents are predominately induced by wind. As wind flows over the lake surface, a portion of the winds momentum is transferred to the

lake surface generating waves, turbulence, large scale circulations and oscillatory motion (seiche), as well as secondary currents (Wetzel et al., 2001). Water movements are then regulated by basin bathymetry, stratification structure and exposure to wind (Wetzel et al., 2001). During ice-cover, wind does not act on the water surface and circulation is largely driven by thermal processes from heat stored in sediment or solar radiation (Kenney, 1996), as well as seiching induced by oscillation of the floating ice sheet (Malm et al., 1998), although river input/output may also play a role if the river is large relative to the size of the lake (Bengtsson, 1996). During lake trout egg incubation, embryos will be exposed to varying lake current velocities during both open-water and ice-covered seasons. Currents during open water season are typically 2% of the wind speed (i.e., 0.2 m s⁻¹ current when wind speed is 10 m s⁻¹), whereas under the ice, oscillation and thermal processes result in much lower currents on the order of mm s⁻¹ (Malm et al., 1998). Alexie Lake has minimal inflows and outflows (Healey and Woodall, 1973), and current effects are likely localized to the immediate inlet and outlet areas (Bengtsson, 1996). Therefore, wind-driven currents, from the period of spawning until the lake is frozen, will be most influential for lake trout embryonic survival, developmental rate, and hatching date.

Spawning sites containing clean substrates within the 3–15 cm size range appear to be innately selected by lake trout (Marsden et al., 1995; McAughey and Gunn, 1995; Sly, 1988), presumably because this size allows for interstitial spaces in the cobble matrix large enough for lake trout eggs to fall in between, but small enough to provide protection from egg predators. In Alexie Lake, the majority of spawning substrate fell within the norms of what has been found in other lakes (between 3 and 15 cm; Martin and Olver,

1980). Although we did observe significant variability in substrate size among spawning sites, there appears to be a minimum size requirement, as only 1% of substrates found on spawning shoals was <3 cm. Small diameter substrates likely do not provide adequate interstitial spacing for egg incubation. Interstitial depths in Alexie Lake varied among as well as within sites, but each spawning shoal had at least one location with interstitial depths of ≥ 25 cm. Similar interstitial depths (>20 cm) were measured at spawning sites in the Laurentian Great Lakes (Marsden et al., 2005). Further, we observed that the upper 25 cm of the substrate matrix was generally uniform in size, meaning substrate size at the surface was a good indicator of substrate throughout. Interstitial depths may be a more important feature of lake trout spawning shoals in northern lakes, where ice depths can reach >2 m (Duguay et al., 2003). Suitable lake trout spawning habitat in Alexie Lake was in water <2 m deep during this study, therefore, deep interstitial depths would be critical to allow embryos to incubate below maximum ice depths. The narrow depth range at which lake trout spawn in Alexie Lake (1–2 m) also makes these sites particularly susceptible to water level fluctuations that may arise from water withdrawal demands for industrial development (Cott et al., 2008) or hydrological regime shifts due to climate change (Wantzen et al., 2008) and are known to affect lake trout reproduction (Wilton, 1985).

High variation in embryonic survival was observed among lake trout spawning sites, suggesting that a large gradient in habitat quality exists within a given lake. Based on the general model of salmonid reproduction, we predicted that lake trout embryonic survival would be a function of wind exposure. For example, in a closely-related species, brook trout (*Salvelinus fontinalis*), where spawning occurs at sites of groundwater

upwelling in lakes, embryonic survival and development rate are a function of groundwater flow (Blanchfield and Ridgway, 2005). Surprisingly, no relationship between wind exposure and embryonic survival was found in Alexie Lake. In fact, some of the highest (75%) and lowest (2%) values for lake trout embryonic survival occurred at different sites that received similar wind exposures. Similarly, Fitzsimons and Marsden (2014) also found no relation between embryonic survival and the loss of artificial eggs, a surrogate for the effect of currents, in Lake Champlain. In our experiment, eggs were incubated on top of the spawning shoals rather than within the interstices, but physical habitat characteristics may have influenced the movement of water to the incubators and were also included as predictors of embryonic survival; none of which were found to influence embryonic survival.

We chose this specific linear fetch model to predict wind exposure because it has been successful in previous lake trout spawning habitat studies (Bigelow, 2009; Flavelle et al., 2002). Linear fetch models are also easy to apply and require only a few input parameters (e.g., water depth, slope, fetch length, and wind speed) and should give reliable estimates of wave parameters and wave exposure in the nearshore zones of lakes. Although easy to use, the linear fetch model may have been too simplistic to predict the full extent of wave driven currents in a complex system like Alexie Lake, which is relatively small, is surrounded by boreal forest, and contains 35 islands thereby limiting fetch. Seibt et al. (2013) found that the linear fetch model performs better in simple systems with no islands, while a non-linear Simulating Waves Nearshore (SWAN) model would be better suited for more complex lakes. The location of the weather station may not have produced real-time data indicative of wind exposure for all spawning shoal sites

sampled in Alexie Lake. This is further supported by the observation of swirling wind patterns during field sampling (P. Blanchfield, personal observation). This unpredictability may be more common at northern latitudes, where gradual topography and shorter tree heights reduce wind sheltering effects on lake wind patterns and may result in greater wind affected areas (Markfort et al., 2010) and increased spatial variability (Podsetchine and Schernewski, 1999). Future research should employ direct measurement of current velocities on spawning shoals to avoid potential pitfalls of inferred current velocities from fetch models. Our on-site wind measurements should generally predict wind conditions better than measurements taken off-site, such as from the nearest urban centre (as done by Fitzsimons and Marsden, 2014; Flavelle et al., 2002; Martin, 1957). Therefore, we believe the modelled wind exposure to be indicative of general wind conditions at Alexie Lake during the spawning season and to be a reasonable estimate for wave induced currents from which to test whether lake trout embryonic survival is a function of wind exposure.

Wind may influence embryonic survival in other ways, such as development rate and hatch success. For example, an in situ brook trout egg incubation experiment found that after a minimum groundwater discharge requirement was met, survival did not increase; however, the proportion of eggs hatched increased linearly as groundwater discharge increased (Blanchfield and Ridgway, 2005). Lake trout embryos in our study showed no signs of development to the stage of emergence (e.g. failed escape), likely because we planted the incubation trays towards the end of the spawning season (to avoid disturbance of natural spawning), and for logistical reasons we collected them approximately one month prior to predicted hatch date. As a result, incubating eggs were

exposed to wind-induced currents for only a six-week period prior to formation of surface ice. Even lake trout eggs deposited at the start of spawning, a month prior to the incubation study, would have been exposed to wind-induced currents for a period of 10 weeks. Although we cannot discount the effect wind exposure may have on development rate and hatch success, it is likely that wind exposure is beneficial in moving lake trout eggs into the interstices of spawning substrate, thereby lessening their exposure to potential egg predators.

The unpredictable nature of wind and abundance of suitable habitat may favour lake-wide spawning by lake trout as a bet-hedging strategy. Fitzsimons and Marsden (2014) suggest that due to environmental stochasticity, optimal conditions for embryonic survival may vary spatially and temporally within a spawning shoal. Lake trout may overcome this using a bet-hedging strategy of broadcasting eggs over a gradient of physical and chemical conditions on a spawning shoal to ensure reproductive success (Fitzsimons and Marsden, 2014). Based on the findings from this study, we believe this idea may be expanded more broadly to include a strategy whereby lake trout broadcast eggs among multiple spawning shoals, either as individuals or as a population, to ensure reproductive success. We submit that diversifying the spatial, physical, and chemical characteristics of spawning habitat, to increase the overall portfolio performance of reproductive success (Moore et al., 2010), may be a tactic used by lake trout to buffer the unpredictable nature of wind and weather conditions in northern regions. This bet-hedging strategy would thereby increase the probability of yearly recruitment to the population and challenges the conventional thought that lake trout spawning site selection is driven by predominate wind.

Chapter 3: Lake Trout Reproductive Strategies

3.1 Introduction

The evolution of animal mating systems is comprised of the relative contributions of sexual selection (Andersson, 1994), parental care (Trivers, 1972) and the spatial and temporal distribution of resources and mates (Emlen and Oring, 1977). In many species, males optimize their reproductive fitness by mating with multiple females. By contrast, the optimal mating rate of females is limited by the production of progeny per mating event (Bateman, 1948). This high energetic investment in gametes by females relative to males often results in conventional sex roles, whereby females provide parental care and males compete for access to females (Kokko and Jennions, 2008). Because parental care is less common in fishes (only found in 21% of families; Blumer, 1982) compared to other vertebrates, the strength of sexual selection and the overall evolution of their mating systems should be driven by the spatial and temporal distribution of resources and matings (Emlen and Oring, 1977).

Salmonine fishes (salmons, trouts and chars) are typically observed in a site-based competitive mating system where males compete for access to females, which is thought to be the limiting resource for male reproductive success (Gross, 1984), while females compete for territories to establish and prepare their spawning sites (Fleming, 1998). Females construct a nest (a series of pits termed a redd) and deposit eggs that are fertilized externally by one or more males. Limited numbers of suitable spawning sites and variability in spawning site quality results in females becoming very selective when choosing their redd sites (Blanchfield and Ridgway, 2005; de Gaudemar, 1998; Esteve, 2005). Males will fight for proximity to females, with body size and exaggerated body

shape being the main factors in establishing dominance hierarchies (Fleming and Gross, 1994; Quinn and Foote, 1994). Paternity tests have shown that the closest male to the female generally fertilizes the greatest proportion of eggs (Blanchfield et al., 2003; Mjølnerød et al., 1998). Thus, proximity to females increases fertilization success. As a result, male reproductive success is maximized quantitatively, by mating with as many females as possible; whereas female reproductive success is maximized qualitatively, by choosing high quality redd sites and males (de Gaudemar, 1998).

The reproductive behaviours of lake trout (*Salvelinus namaycush*) sharply contrast the typical salmonine mating system described above (Esteve et al., 2008; Gunn, 1995; Muir et al., 2012). Spawning usually takes place in lakes on wave swept shoals, and unlike all other salmonines, lake trout do not provide any parental care (i.e., no redd is constructed by the female; Martin and Olver, 1980). Eggs are spawned directly onto clean substrate, where they fall into interstitial spaces and incubate for several months before emerging (Royce, 1951). Also, lake trout do not display overt male-male agonistic behaviour (Esteve et al., 2008; Gunn, 1995; Royce, 1951), a predominant behavioural characteristic of the Salmoninae subfamily (Esteve, 2005). Further, females do not show territorial behaviour (i.e. redd defense) or obvious mate selection (Esteve et al., 2008). However, there are some similarities in reproductive behaviour between lake trout and other Salmonine fishes, including males arriving earlier on breeding grounds and staying longer than females each year (Martin and Olver, 1980; Miller and Kennedy, 1948; Muir et al., 2012; Royce, 1951).

Lake trout are a long-lived, iteroparous species that typically spawn in lakes during the fall (Gunn, 1995). Migration from the offshore summer refuge onto nearshore

spawning shoals generally coincides with surface water temperatures declining to 12° C or lower (Redick, 1967). Preferred spawning habitat is selected along exposed shorelines off points, islands or on mid-lake shoals containing clean substrate including pebble and cobble mainly 3-15 cm in diameter (Martin and Olver, 1980; See Chapter 2). Spawning normally occurs during nighttime (Gunn, 1995) but has been observed during the day (Binder et al., 2015; Esteve et al., 2008; Muir et al., 2012). Males often constitute 60–85% of annual spawning populations, resulting in highly skewed operational sex ratios on spawning shoals. This imbalance is thought to be a product of earlier maturation, early arrival and longer duration on spawning grounds and the increased likelihood of males spawning each year (Eschmeyer, 1955; Martin, 1957; Miller and Kennedy, 1948).

Lake trout reproductive behaviour is relatively understudied when compared to other salmonines, and what literature exists is largely from the southern extent of its geographic range (Muir et al., 2012). In general, information on the timing of movement onto spawning shoals and the degree of movements among spawning sites for males and females at seasonal and daily scales remains an important knowledge gap. Furthermore, few studies have investigated reproductive strategies of lake trout (Esteve et al., 2008; Muir et al., 2012).

The objectives of this chapter are three-fold: (i) to determine when and where lake trout spawn in a typical northern boreal lake; (ii) to describe sex-specific timing and movements of lake trout over the duration of a spawning season; and (iii) to test if male and female lake trout spawn at multiple locations in Alexie Lake. I predict the abundance of suitable habitat and the unpredictability of habitat quality in Alexie Lake (See Chapter 2) results in both male and females spawning at multiple sites to spread the risk of

choosing poor spawning habitat and increase overall reproductive success. Using data collected from a whole-lake acoustic telemetry array, I will present the movements of five male and six female lake trout over the course of the 2013 spawning season. A spatial temporal clustering analysis was used to determine when and where lake trout formed spawning clusters. These data provide new insights into the reproductive strategies of male and female lake trout and further our knowledge on spawning site use for managing this iconic Canadian fish species.

3.2 Methods

3.2.1 Study Site

The study was conducted in Alexie Lake (62° 40' N, 114° 05' W), located approximately 30 km northeast of Yellowknife, Northwest Territories, Canada (Fig. 3.1). Alexie Lake is a medium size (area: 402 ha, maximum depth: 32 m, mean depth: 11.7 m) oligotrophic lake, possessing 35 islands and a shore length of 28 km. Stratification occurs during the summer until September when the lake becomes isothermal (Guzzo, et al., 2015; Healey and Woodall, 1973). Alexie Lake's size, physical, and limnological characteristics are considered "typical" for lake trout lakes (Gunn et al., 2004). Alexie Lake contains four large-bodied species; lake trout, northern pike (*Esox lucius*), lake whitefish (*Coregonus chupeaformis*) and burbot (*Lota lota*) as well as numerous prey fish species (see Cott et al., 2011). Alexie Lake is a designated research lake that is closed to fishing.

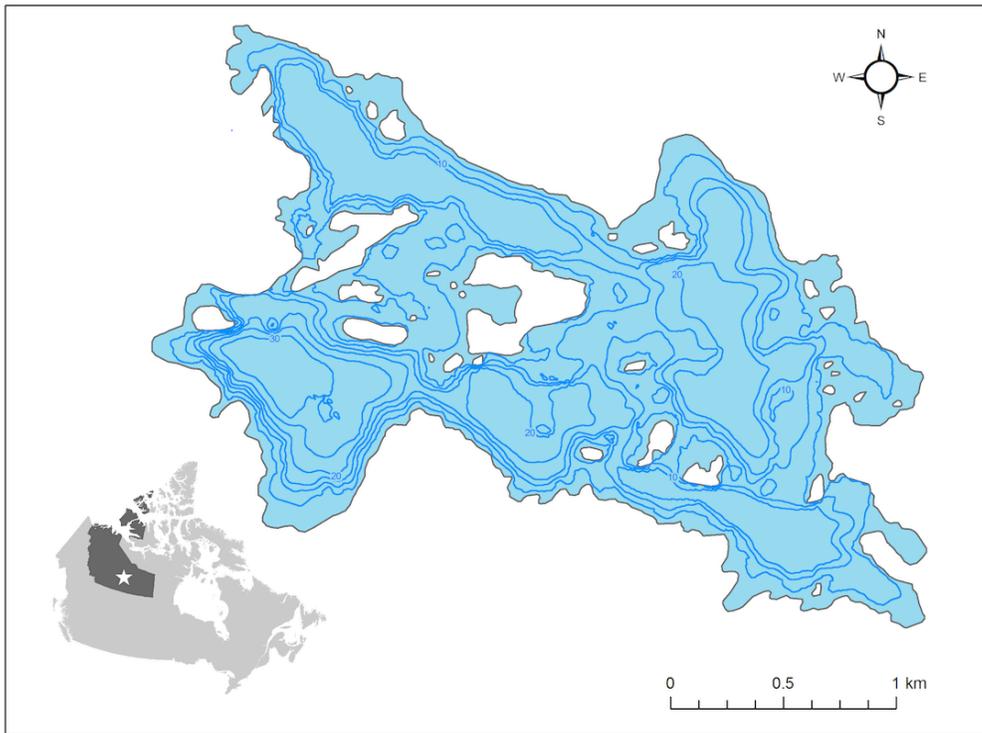


Figure 3.1 – Alexie Lake is located 30 km Northeast of Yellowknife, NWT. The bathymetric contours are at 10 m increments.

3.2.2 Lake water temperature

Water temperature in Alexie Lake was recorded hourly on HOBO® Pendant™ temperature loggers (Onset® Computer Corporation, Borne, MA) set in the deepest basin at 0.5 m, at 1 m depth intervals from 1 m to 20 m and at 25 m and 30 m below the water surface. Mean daily temperature for each depth was calculated followed by a spline interpolation to obtain temperatures for every 0.1 m depth interval from lake surface to bottom. Interpolated daily temperature profiles were used to estimate water temperatures occupied by lake trout implanted with pressure-sensing telemetry transmitters (see Guzzo, et al., 2015; Plumb and Blanchfield, 2009), and determine the role of water temperature in the annual timing of spawning.

3.2.3 Lake bathymetry

A high-resolution hydroacoustic survey was conducted in June 2012 (Milne Technologies, Keene, ON, Canada) producing a detailed bathymetric raster (2.5 x 2.5 m). Hydroacoustic data were collected using a 120 kHz Simrad EK60 7.0° split-beam echo sounder system following a systematic parallel survey design with transects 25 m apart (for details see Cott et al., 2015). These data were used to determine the bathymetric depth for each lake trout telemetry position (see below). This in conjunction with the pressure sensor reading (see below) allows the determination of fish depth from the lake bottom.

3.2.4 *Fish acoustic telemetry*

Five male (fork length range: 478–525 mm, weight range: 1193–1535 g) and six female lake trout (fork length range: 466–557 mm, weight range: 1067–1840 g) were tracked during the 2013 spawning season (approximately the month of September). All lake trout were captured by angling with a barbless lure in the spring (June 12–13, 2013) when surface water temperature was $<15^{\circ}$ C. Once captured, lake trout were brought to shore in holding containers, lightly anesthetized in a solution of 90 mg L^{-1} Tricaine Methanesulfonate buffered with sodium bicarbonate and surgically implanted with a coded acoustic transmitter with pressure (for depth) and accelerometer (for activity) sensors that randomly emitted an acoustic signal every 80–160 s (V13AP-1L, tail beat algorithm; VEMCO, Ltd., Bedford, NS, Canada). See Blanchfield et al. (2005) for details on surgical procedures. Transmitters were 13 mm in diameter, 44 mm in length, and weighed 6 g in water. Each transmitter's depth sensor was individually calibrated at 4 m depth intervals from the surface to lake bottom in Alexie Lake, and were accurate to ± 1.7 m.

The spatial positions of lake trout implanted with acoustic transmitters were monitored using a VEMCO Positioning System (VPS; VEMCO Ltd.) — a fine-scale positioning system used for tracking aquatic animals. The VPS uses hyperbolic positioning, also known as multilateration, which measures the time difference on arrival (TDOA) of a signal from a transmitter at three or more time-synchronized receivers (Smith, 2013). An array of 72 underwater omni-directional acoustic receivers (VR2W, VEMCO Ltd.) with a mean distance of 201.4 m (range: 120.4m–311.9m) between

receivers was deployed in Alexie Lake to monitor lake trout during spawning behaviour 2013 (see Appendix for further details).

3.2.5 Acoustic telemetry data filter

Prior to analyses, telemetry positions were filtered to ensure that only the highest quality data were used to examine lake trout spawning behaviour. First, positions with successive timestamps less than the minimum interval (80 s) for each individual fish were removed as these positions were assumed to be false positions. Second, lake trout positions greater than 2.5 m (size of one raster grid) outside of the lakeshore were removed. The additional 2.5 m buffer outside of the lakeshore was applied because lake trout are known to spawn in the nearshore area of Alexie Lake (see Chapter 2) which is also a region of increased telemetry error (see Appendix), thus the additional buffer retains valuable spawning data. Third, lake trout depth data had to be greater than or within 2 m of the lake bottom to encompass pressure sensor error (± 1.7 m). Fourth, only successive positions less than realistic lake trout swimming speeds (< 1.2 m s⁻¹; Font, 2015) were included. Finally, I conducted stationary tag trials using VEMCO V13-1P tags with random signal transmission between 10 s to 30 s on known nearshore spawning shoals. I calculated the twice the distance root mean squared (2DRMS) for each estimated stationary tag position, relative to their known location in order to develop a relationship between measured error and hyperbolic positioning error (HPE), a unitless estimate of positioning error provided for each spatial position estimated by the VPS (See Appendix for further details). Using the relationship between 2DRMS and HPE for stationary tag data, I determined that removing all data with an HPE > 106 would result in 95% confidence that our data has measurement error less than 27 m, which was determined to

be sufficient for our cluster analyses (see Appendix). After filtering, 87% of the original dataset was retained.

3.2.6 Movement metrics

The spawning season was defined as the period between August 30 (day after the 15° C isocline broke; see below) – September 30 (estimated end date; but see below). Using movement data of individual male and female lake trout collected during the spawning season, I calculated mean daily (1) distance travelled (m), (2) acceleration (m s^{-2}), to calculate energy expenditure and activity, and (3) daily persistence index (PI), defined as the mean cosine of turning angles (unitless) to determine the linearity of movements. The PI ranges from -1 to 1, where a PI = 1 corresponds to linear or directed movement, PI = 0 corresponds to uncorrelated and therefore more tortuous movement, and PI = -1 corresponds to movements that oscillate back and forth (Laidre et al., 2012).

3.2.7 Spatial temporal clustering analysis

Spatial temporal cluster analysis was performed using the density-based clustering algorithm, Spatial Temporal Density-Based Spatial Clustering of Applications with Noise (ST-DBSCAN; Birant and Kut, 2007) to determine areas in Alexie Lake where individual lake trout remained for significant periods of time during the spawning season (while spawning, feeding, or resting). The spatial temporal clustering algorithm requires data points with three required fields: x coordinate, y coordinate and timestamp. Additionally four parameters are required to create clusters: epsilon distance—the Euclidean distance parameter for spatial attributes; epsilon time—the Euclidean distance parameter for time attributes; minimum points—the minimum number of points required to create a cluster;

and $\Delta\epsilon$ —the acceptable change in time between the current cluster mean and the potential new addition to the cluster. Model parameters were estimated using a simple heuristic described by Ester et al. (1996) and Birant and Kut (2007) with my data (See Appendix for further details on parameter estimation). Parameters estimates were as follows: epsilon distance = 41 m; epsilon time = 3254 s; minimum points = 9; and $\Delta\epsilon = 2$ SD. Details on the refinement of these data to determine whether clusters represent spawning activity are described below.

3.2.8 Spawning activity determined by cluster filtering

The spatial temporal clustering algorithm is non-biased towards the behaviour of the fish during the cluster formation. This means that when individual fish cluster, it could represent a number of different behaviours, such as spawning, feeding or resting. Therefore, filtering was required to identify potential spawning clusters. Because lake trout spawn nearshore at shallow depths (~2 m) during the month of September in Alexie Lake (see Chapter 2; personal observation), I used distance to shore and depth contour occupied as a filter for identifying potential spawning clusters. This was done as follows. I plotted kernel density estimates (KDE) of distance to nearest shore occupied by male and female lake trout (see Fig. 3.4), which indicated that males remain closer to the shore during the spawning season. It is well documented that males come onto the spawning shoals first and remain longer than females (Martin and Olver, 1980; Miller and Kennedy, 1948; Muir et al., 2012; Royce, 1951), so I selected a 50 m distance to shore criterion based on the visual inspection of the male distance to nearest shore KDE. I also plotted the KDE of contour depth occupied by male and female lake trout and found a bimodal distribution for males (see Fig. 3.3). The shallower depth contour KDE mode is

likely potential spawning males on spawning shoals and therefore I included a criterion of <4 m depth contour. In order to be considered a potential spawning cluster, >50 % of the detections within a given cluster must have met both criteria (i.e., distance to shore <50 m and depth contour <4 m).

Sites where potential spawning clusters formed were considered spatially unique when the cluster centers were >70 m apart. This spatial criteria was based on mean distance between the center of known spawning shoals along a 780 m stretch of an Alexie Lake shoreline (site 1; see Chapter 2). Male lake trout often aggregate on spawning shoals but show very little behavioural activity other than when slowly swimming along the edge of the shoal, however; when one or more females approach a male aggregation, a frenzy of activity ensues (Binder et al., 2015; Esteve et al., 2008; Muir et al., 2012, D. Callaghan personal observation). To distinguish between these low and high activity periods on spawning shoals, I categorized spawning clusters as low or high activity clusters based on whether the maximum acceleration recorded during a specific cluster was greater or less than 1.3 m s^{-2} . This criterion was determined from the mean acceleration of all clusters (spawning and non-spawning; $n = 4622$) + 2 standard deviations (SD).

3.2.9 Spawning cluster metrics

Spawning clusters were used to determine the timing of lake trout spawning, where the onset and conclusion of the spawning season were defined as the earliest and latest occurrence of a spawning cluster, respectively. Peak spawning was determined as the earliest and latest date where the daily number of spawning clusters was greater than

or equal to half the maximum number of daily spawning clusters. To determine if lake trout were spawning during the day or night, I used the *crepuscule* function from the *maptools* R package (Bivand and Lewin-Koh, 2015) to define periods of day, night, dawn and dusk for Alexie Lake, NWT, during the spawning season. Spawning cluster metrics were calculated for each individual fish and summarized into mean and standard deviation for: (1) frequency of spawning cluster formation, (2) total cumulative duration spent in spawning clusters, (3) duration per cluster formation, (4) total spatially unique sites visited, (5) the distance and (6) duration between subsequent spawning clusters, (7) frequency of cluster formations with low activity (site visits) prior to first high activity cluster (spawn event). Minimum convex polygons (MCP) were calculated using the *mcp* function from the *adehabitatHR* R package (Calenge, 2006), to determine the spatial spread of lake trout spawning clusters.

3.2.10 Statistical analysis

All analyses were completed in R V.3.2.1 (R Core Team, 2015). Kernel density estimates (KDE) were computed for distance to shore, depth contour occupied, and depth occupied by lake trout using the *density* function in R. The resulting KDE's were multi-modal; therefore, mode means of the KDE's were determined using the *normalmixEM* function, an Expectation-Maximization (EM) algorithm for mixtures of normal distributions, from the *mixtools* R package (Benaglia et al., 2009). Mean times and standard deviations of all and high activity spawning clusters were calculated with the *circadian.mean* and *circadian.sd* functions from the *psych* R package (Revelle, 2015) that calculates the circular mean of circadian data. Using spawning cluster formation start times for all spawning clusters and high activity spawning clusters, I tested whether lake

trout spawn during the night or day using a Pearson's Chi-square test. Using the *loess* function in R, I applied a LOESS (local polynomial regression) curve fitting smoother to the frequency of lake trout spawning by binned one-hour segments for all spawning clusters (both high and low activity) and high activity spawning clusters to show the general spawning time trends. A non-parametric Wilcoxon rank sum test was used to test differences in, daily displacement PI, acceleration and site visits prior to spawning between sexes. A log transformation was applied to cluster formation frequency, total duration, mean duration, site visits, distance and duration between consecutive clusters, and minimum convex polygon area data to meet parametric assumptions prior to testing differences between sexes, activity state (high or low) and the interaction of sex and activity state using a type III two-way ANOVA. We used $p < 0.05$ to determine statistical significance for all datasets.

3.3 Results

3.3.1 Spatial distribution of lake trout

The migration of both male and female lake trout from the deeper offshore to shallower nearshore regions of Alexie Lake corresponded to the breakdown of the 15°C isocline (August 29, 2013; Fig. 3.2). A clear bimodal depth distribution was apparent for both males and females during the spawning season, with males distributed around mean depths of 1 m and 12 m and females distributed around mean depths 2 m and 14 m. Telemetry-tagged male lake trout occupied areas of Alexie Lake where mean lake depths were 3 m and 17 m while females occupied mean lake depths of 5 m, 18 m, and 29 m (Fig. 3.3).

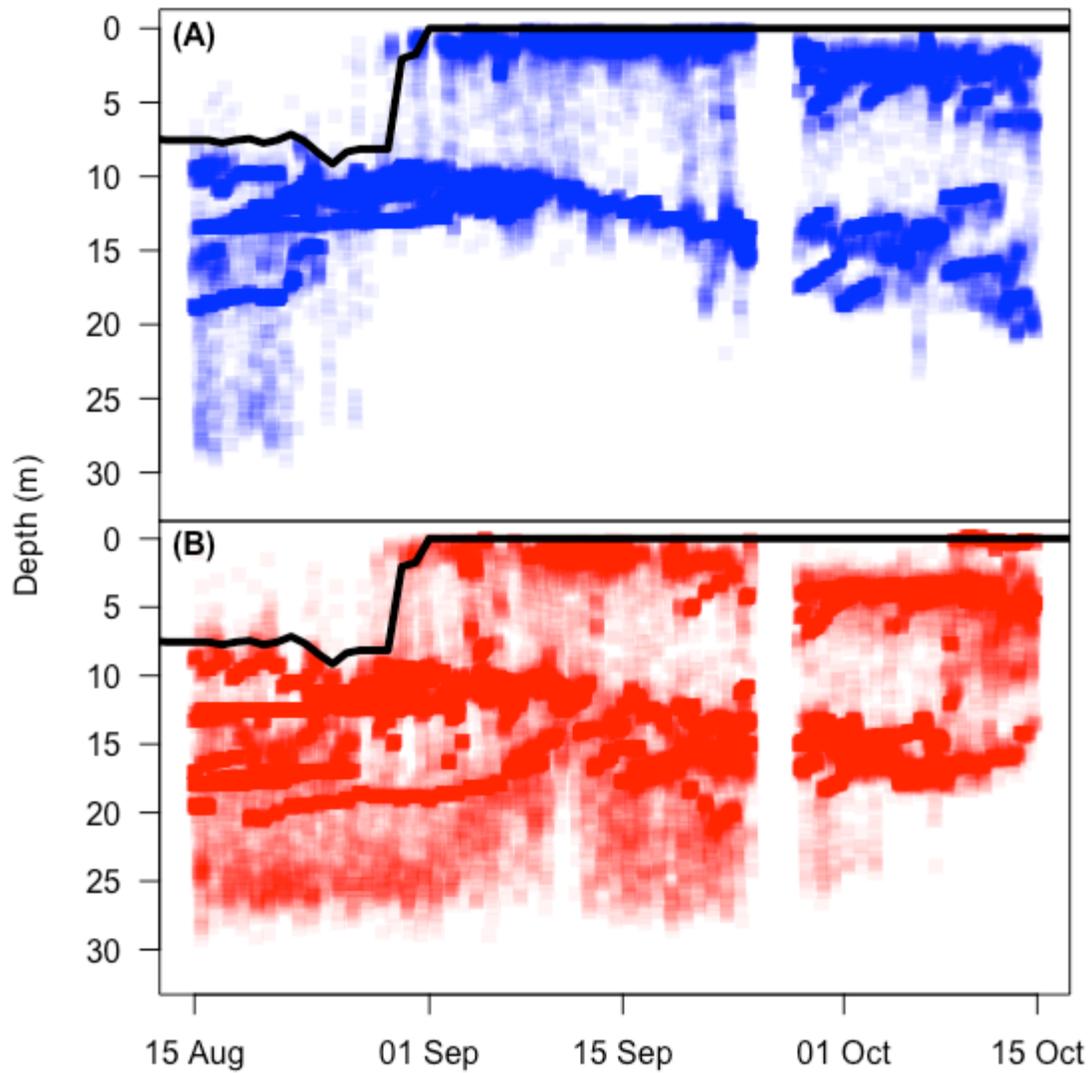


Figure 3.2 – Depth distribution of males (A) and females (B) during the spawning season in Alexie Lake, NWT. The black line represents the 15° C isocline. Points were given transparency value of 5%, therefore the darker the colour the higher the density of points. No data are available between September 25-27, 2013, while the VPS was removed from the lake for download.

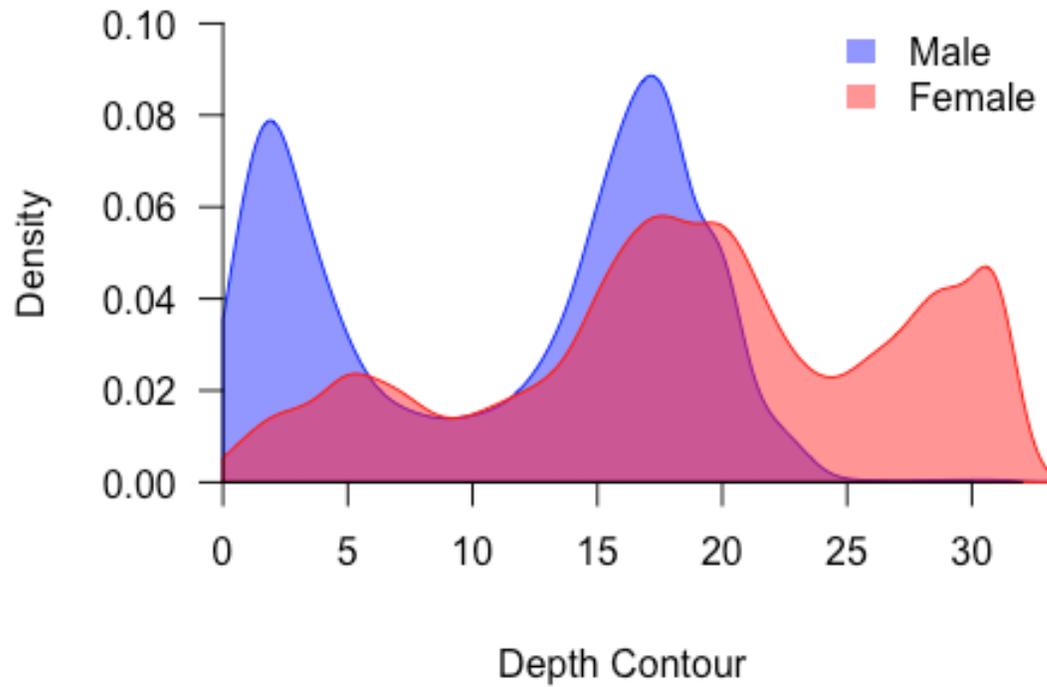


Figure 3.3 – Kernel density estimate of bottom contour depth occupied by male (blue) and female (red) lake trout in Alexie Lake, NWT, between August 30 and September 30, 2013.

The spatial distribution of lake trout in Alexie Lake differed between sexes during the spawning season. Males had a higher density of detections in the nearshore region than females (Fig. 3.4 and 3.5). Males exhibited a clear peaked mode at a mean distance from shore of 14 m, and a second mode at a mean distance from shore of 131 m (Fig. 3.4). Female lake trout exhibited three modes at mean distances from shore of 28 m, 72 m, and 127 m, but none showed the same high density as males (Fig. 3.4).

3.3.2 Spatial distribution of spawning clusters

A total of 226 lake trout spawning clusters were estimated using the spawning cluster analysis, of which 124 (55%) were classified as high activity clusters and more likely to have spawning behaviour taken place (Fig. 3.6). Spawning clusters were found throughout the nearshore region of Alexie Lake, covering an area of 4.26 km² (based on MCP).

3.3.3 Timing of spawning

All five males formed spawning clusters, while five of six females investigated formed spawning clusters; LT-32 never formed a spawning cluster in 2013 and was designated a non-spawning female (see Fig. 3.7). Lake trout showed a wide range in timing of spawning cluster formation, with males spending 4–25 days on spawning shoals compared to only 2–9 days by females. Most individuals (80%) were present during peak spawning, but two individuals, LT-31 (male) and LT-38 (female) only formed spawning clusters early in the season prior to peak spawn and did not return during or post peak spawn.

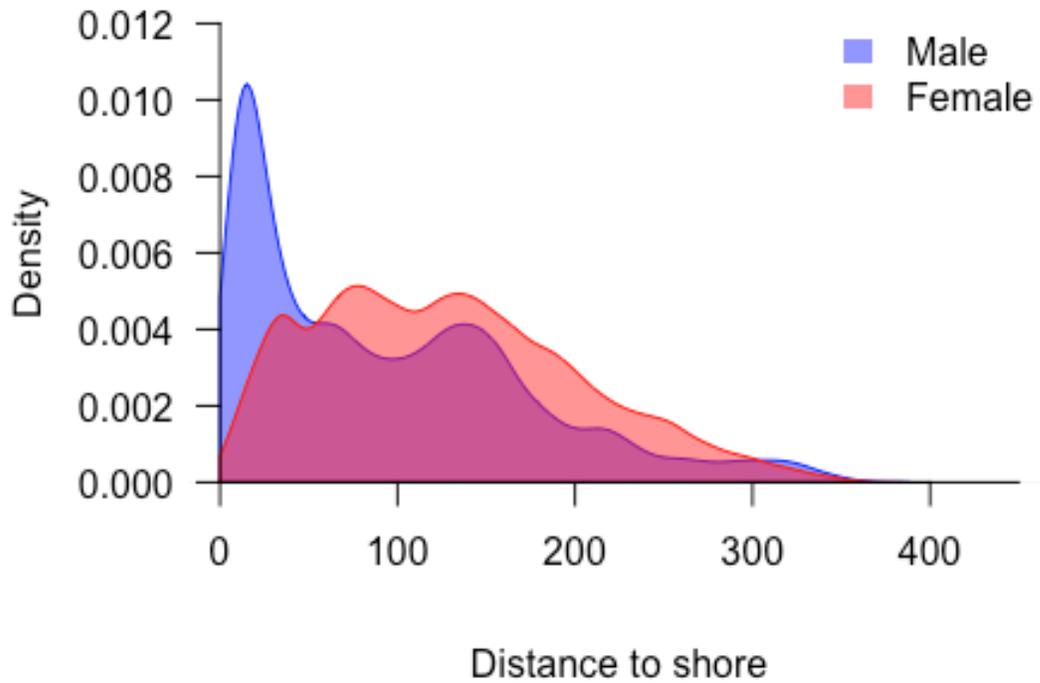


Figure 3.4 – Kernel density estimate (KDE) of distance to nearest shore occupied by male (blue) and female (red) lake trout in Alexie Lake, NWT, between August 30 and September 30, 2013.

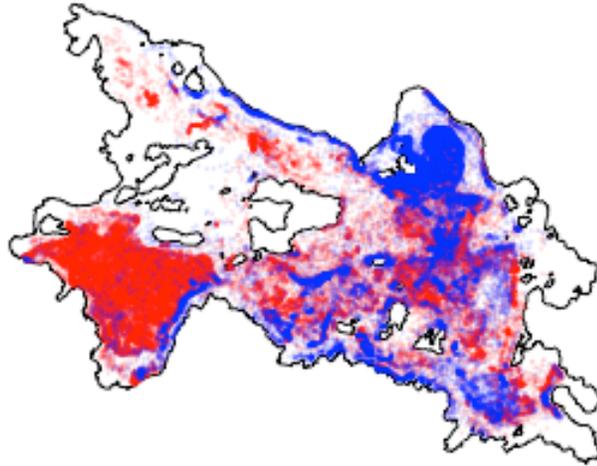


Figure 3.5 – Male (blue), and female (red) lake trout positions during the 2013 spawning season in Alexie Lake, NWT. Points were given transparency value of 10%, therefore the darker the colour the higher the density of points

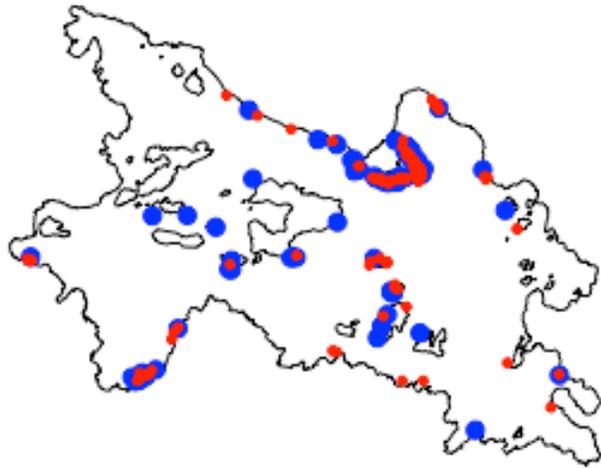


Figure 3.6 – Lake trout spawning clusters in Alexie Lake, NWT during the 2013 spawning season. The smaller red circles represent the center of high activity clusters and larger blue circles represent the center of low activity clusters

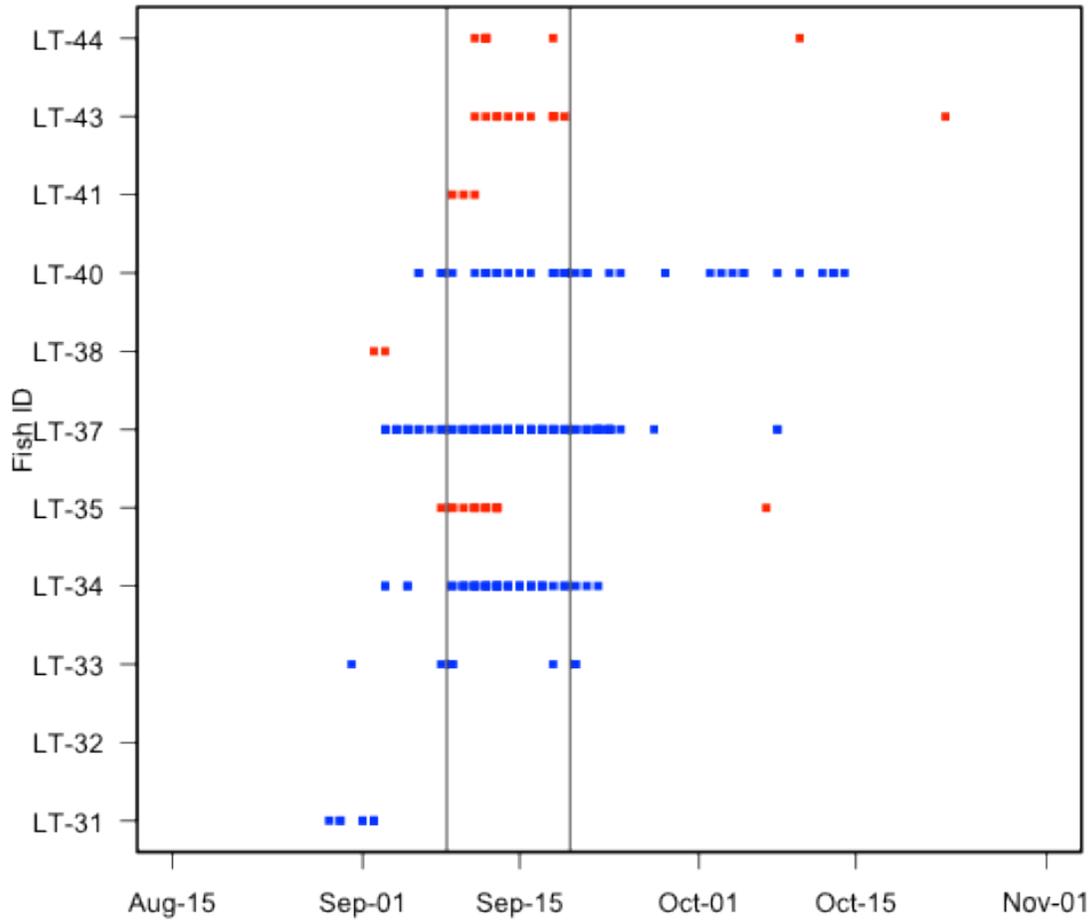


Figure 3.7 – Spawning cluster formation by individual lake trout in Alexie Lake, NWT. Squares represent one or more spawning cluster formed on the date for males (blue) and females (red) and vertical black lines represent the onset and conclusion of peak spawning.

Based on spawning clusters, the onset of lake trout spawning in 2013 was August 29 coinciding with a surface temperature of 15.1 °C (Fig. 3.8). Spawning occurred over a 55 day period and concluded on October 23 when surface temperature was 5.5 °C. Peak spawn began on September 9, and lasted 10 day, concluding on September 19. Surface temperature was 14.6 °C at the start of peak spawn and dropped 3.5 °C over the duration of peak spawn. The maximum number of spawning clusters (20) occurred on September 13. The majority of all spawning clusters (61%) and high activity spawning clusters (65%) occurred during peak spawn. The frequency distributions of total, high activity, and low activity spawning cluster were similar (Fig. 3.8). Peak spawning for male and female lake trout occurred at similar dates, with peaks occurring on September 13 and September 12, respectively (Fig. 3.9). Collectively, males remained on the spawning shoals for a maximum of 25 consecutive days while females spent a maximum of 8 consecutive days.

Lake trout showed a significant preference for spawning during the night; 65% of high activity spawning clusters occurred at night (Pearson's Chi-squared Test: $X^2 = 10.45$; $p = 0.001$). Further, when considering all spawning clusters (both high and low activity clusters), lake trout also show a significant preference for night spawning ($X^2 = 3.98$; $p = 0.046$; Fig. 3.10). Mean cluster formation occurred at 22:42 ± 1.9 h (mean ± SD), and high activity spawning clusters occurred at 22:21 ± 1.5 h. The maximum number of spawning clusters ($n = 19$) occurred between 19:00–20:00, similar to the greatest number of high activity spawning clusters ($n = 13$), which also occurred between 19:00–20:00. The minimum number of spawning clusters ($n = 4$) occurred between

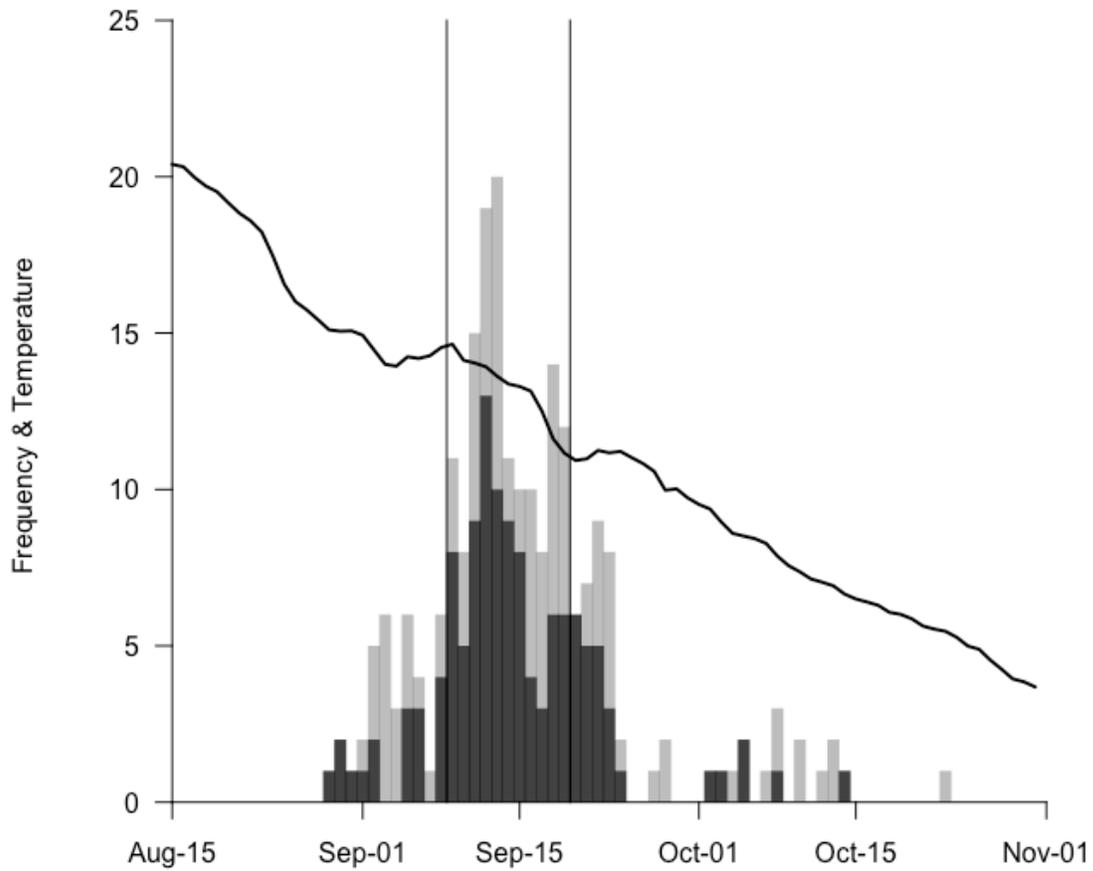


Figure 3.8 – Frequency distribution of spawning clusters over the duration of the 2013 spawning season in Alexie Lake, NWT. Light grey bars represent the cumulative frequency of spawning clusters (both low and high activity), dark grey bars represent high activity spawning clusters, the horizontal black line represents daily surface water temperature ($^{\circ}\text{C}$) and the vertical black lines represent the onset and conclusion of peak spawning.

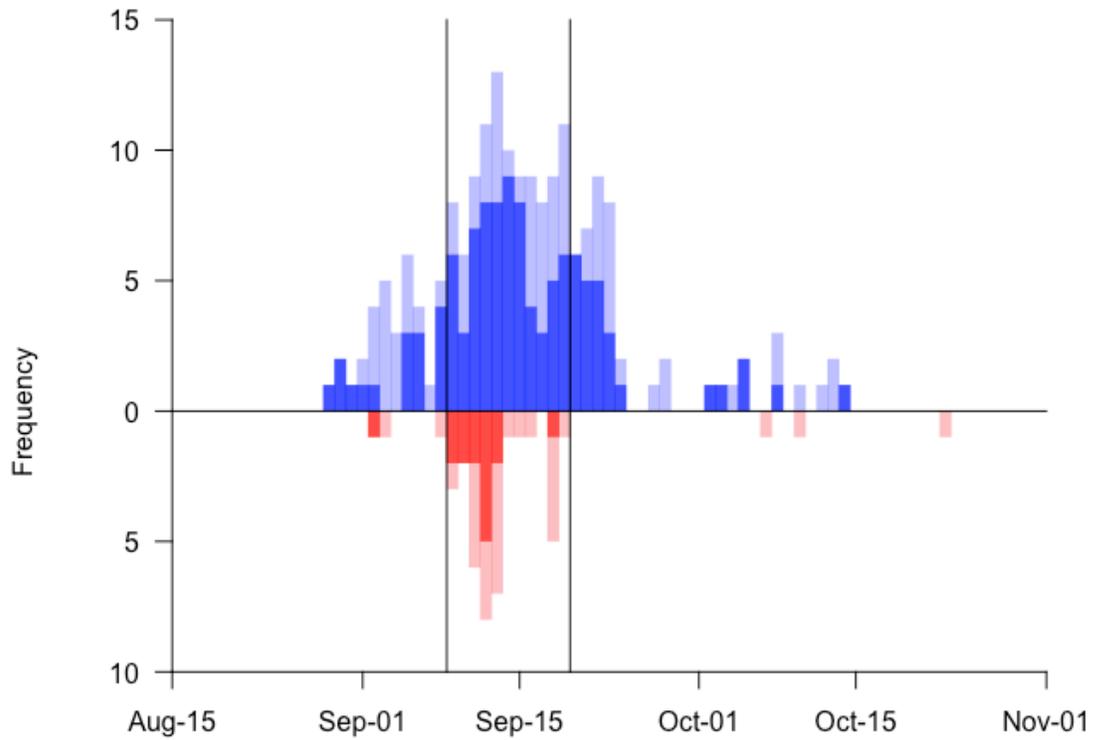


Figure 3.9 – Frequency distributions of male (blue) and female (red) spawning clusters over the duration of the 2013 spawning season in Alexie Lake, NWT. Light bars represent daily cumulative frequency of spawning clusters (both low and high activity), dark bars represent high activity spawning clusters and vertical black lines represent the onset and conclusion of peak spawning.

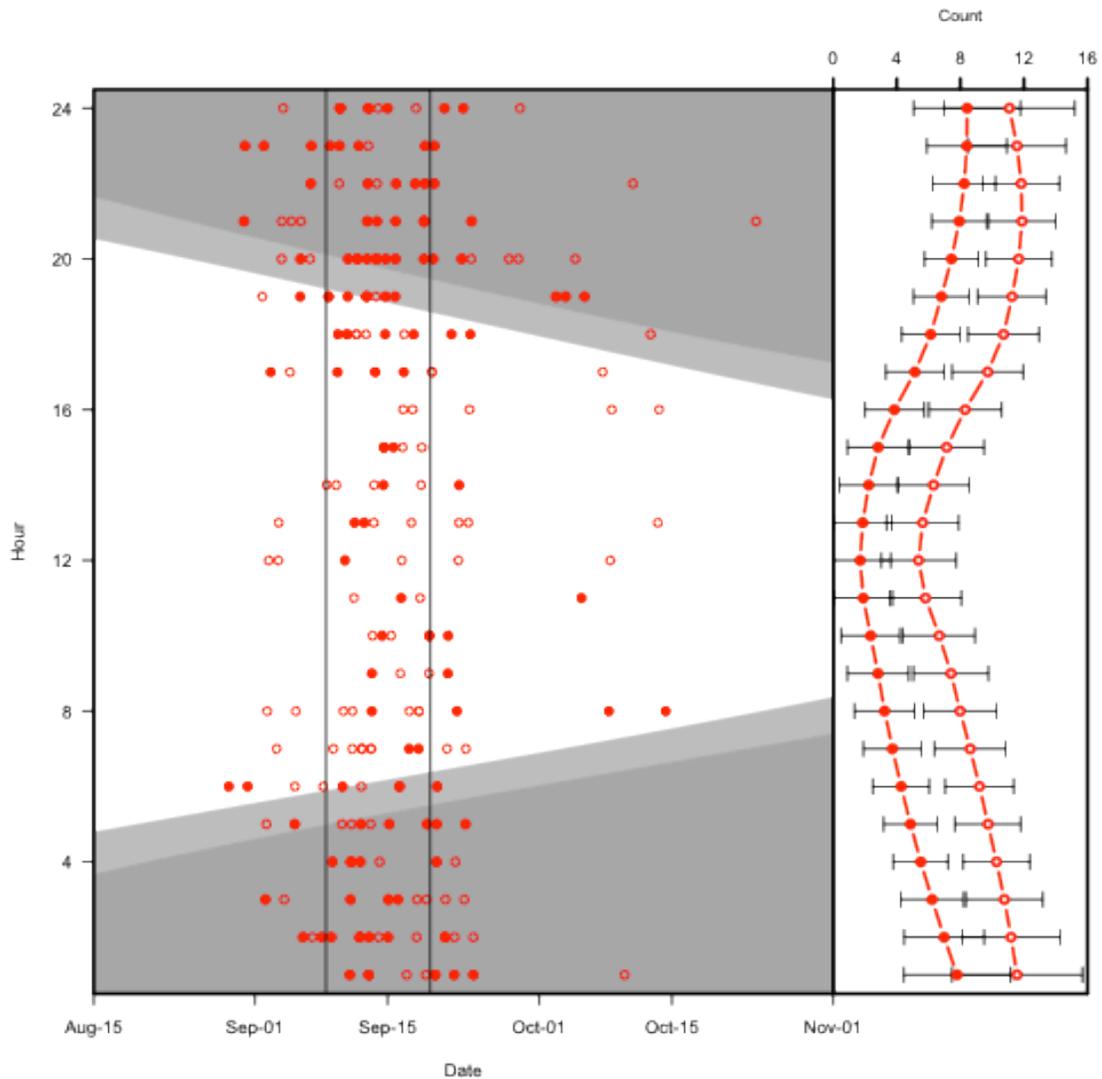


Figure 3.10 – Lake trout spawning cluster formation start times over the duration of the 2013 spawning season (left panel), and summarized as total counts per hour (right panel), in Alexie Lake, NWT. Both low activity (open circles) and high activity (closed circles) are displayed in both panels. Light grey polygons represent dawn and dusk, dark grey polygons represent nighttime and vertical black lines represent the onset and conclusion of peak spawning. The lines in the right panel represent a LOESS trendline with 95% confidence interval error bars.

morning hours of 8:00–9:00 and 10:00–11:00. No high activity spawning occurred between the hours of 15:00–16:00.

3.3.4 Lake trout spawning behaviour

Over the course of the spawning season the daily distance travelled by lake trout was not significantly different between spawning males and females; both sexes moved ~ 7 km per day (Wilcoxon Rank Sum Test: $W = 8.82 \times 10^3$; $p = 0.15$; Table 3.1). The single non-spawning female did show a higher daily displacement of 11.9 ± 2.97 km. Spawning females made more linear movements than males, as indicated by females having significantly higher PI ($W = 6.51 \times 10^3$; $p < 0.001$; Table 3.1). The non-spawning female also made more directed movement, consistent with spawning females but with a greater PI (0.23 ± 0.09 ; Table 3.1). Spawning males exerted significantly more energy than females over the course of the spawning season in spite of similar daily displacements, exhibiting daily acceleration rates that averaged 0.12 m s^{-2} greater than females ($W = 1.20 \times 10^4$; $p < 0.001$; Table 3.1). The non-spawning female also showed similar acceleration as spawning females (0.36 ± 0.08 ; Table 3.1).

Telemetry-tagged male lake trout created a total of 185 clusters, of which 59% were high activity clusters. Females on the other hand created roughly one-quarter of the clusters than males did ($n = 41$ clusters), 37% of which were high activity clusters. Individual male lake trout formed significantly more clusters, on average, than females (ANOVA: $F_{(1,16)} = 8.52$; $p = 0.01$; Table 3.2). No significant difference was found between activity states ($F_{(1,16)} = 0.13$; $p = 0.72$) or the interaction of sex and activity ($F_{(1,16)} = 0.83$; $p = 0.38$).

Cluster duration differed significantly between activity states with lake trout spending 61.7 min more in high activity clusters than low activity clusters ($F_{(1,222)} = 4.27$; $p = 0.04$). No significant differences in cluster duration were found between sexes ($F_{(1,222)} = 0.00$; $p = 0.97$) or the interaction of sex and activity ($F_{(1,222)} = 1.75$; $p = 0.19$), even though males spent on average 43.8 min longer in clusters than females (Table 3.2). Males in total spent significantly more time in spawning clusters (1.4 ± 1.3 d) compared to females (0.5 ± 0.6 d; $F_{(1,16)} = 7.79$; $p = 0.01$). No significant differences in total cluster duration were found between activity states ($F_{(1,16)} = 0.75$; $p = 0.4$) or the interaction of sex and activity ($F_{(1,16)} = 0.86$; $p = 0.37$). Males visited significantly more spatially unique spawning sites than females, visiting five more unique sites on average than females ($F_{(1,16)} = 6.68$; $p = 0.02$). No significant differences in number of site visits were found between activity states ($F_{(1,16)} = 0.02$; $p = 0.9$) or the interaction of sex and activity ($F_{(1,16)} = 0.70$; $p = 0.42$).

Although the distance between consecutive spawning clusters for females was 197.86 m greater than males (Table 3.2), this measure was not significantly different between sexes ($F_{(1,212)} = 1.97$; $p = 0.16$), activity state ($F_{(1,212)} = 0.50$; $p = 0.48$) or the interaction of sex and spawning state ($F_{(1,212)} = 1.01$; $p = 0.32$). Similarly, no significant difference was found for duration between consecutive clusters between sexes ($F_{(1,212)} = 3.42$; $p = 0.07$), activity state ($F_{(1,212)} = 2.84$; $p = 0.09$) or the interaction of sex and activity state ($F_{(1,212)} = 1.75$; $p = 0.19$), despite the observation that duration between female spawning clusters was 52.9 h more than males. Low activity site visits prior to spawning (i.e. high activity site visits) were not found to be significantly different

Table 3.1 – Summary statistics for spawning male, spawning female and non-spawning female lake trout movement metrics during the 2013 spawning season in Alexie Lake, NWT. I report the number of fish (*n*), means and standard deviations of daily distance travelled (km), persistence index (PI), and acceleration ($m\ s^{-2}$).

Sex	n	Daily Distance		
		(km)	PI	Acceleration ($m\ s^{-2}$)
Spawning Male	5	7.02 (3.56)	0.07 (0.18)	0.49 (0.28)
Spawning Female	5	7.5 (3.48)	0.17 (0.17)	0.37 (0.18)
Non-spawning Female	1	11.91 (2.97)	0.23 (0.09)	0.36 (0.08)

Table 3.2: Summary statistics for male and female lake trout spawning cluster data during the 2013 spawning season in Alexie Lake, NWT. For all male and female clusters (both high and low activity clusters) and spawning male and female clusters (high activity clusters), I report the number of fish (*n*), means and standard deviations of clusters formed, cluster duration, unique cluster sites visited, distance between consecutive clusters (*m*), duration between subsequent clusters (*h*), site visits prior to first spawn and minimum convex polygon area of all cluster points (*km*²).

Sex	<i>n</i>	Clusters	Duration (min)	Sites	Distance Between Clusters (m)	Duration Between Clusters (h)	Site Visits Prior to Spawn	MCP Area (km ²)
All Male	5	37.0 (31.9)	168.5 (55.2)	9.2 (6.3)	216.2 (316.6)	15.5 (316.6)	-	1 (0.9)
Low Activity Male	5	15.2 (15.0)	123.1 (61.9)	5.8 (4.1)	235.6 (314.2)	29 (314.2)	-	0.4 (0.5)
High Activity Male	5	21.8 (17.0)	191.7 (54.9)	7.4 (4.5)	257.2 (392.4)	22.2 (41.4)	1.8 (2.7)	0.9 (0.9)
All Female	5	8.2 (6.1)	124.7 (46.5)	4.2 (2.5)	414.0 (442.1)	68.4 (442.1)	-	0.4 (0.4)
Low Activity Female	5	5.2 (5.4)	104.2 (51.3)	3.2 (2.9)	433.5 (461.9)	106.5 (461.9)	-	0.2 (0.3)
High Activity Female	5	3.0 (2.3)	131.1 (51.7)	2.0 (1.0)	348.1 (379.2)	13.7 (12.4)	2.4 (4.3)	0.1 (0.1)

between males and females, each visiting roughly two sites prior to spawning ($W = 12.5$; $p = 1$; Table 3.2). Male spawning site MCP area was on average 0.6 km^2 greater than females (Table 3.2), but was not found to be significantly different between sexes ($F_{(1,16)} = 2.76$; $p = 0.12$), activity state ($F_{(1,16)} = 0.24$; $p = 0.63$) or the interaction between sex and activity state ($F_{(1,16)} = 0.73$; $p = 0.41$).

3.4 Discussion

I have provided a detailed description of the lake trout mating system at the whole-lake scale in a northern lake with typical lake trout characteristics. Using an acoustic telemetry monitoring system and a novel spatial temporal clustering analysis, I was able to quantify lake trout spawning movements and behaviours over the course of an entire spawning season. Lake trout were found to cluster on spawning shoals virtually around the entire nearshore region of Alexie Lake, as well as around several islands, which is consistent with previous findings that suitable spawning habitat is abundant in Alexie Lake (Chapter 2). Consistent with the results of other studies, males arrived earlier than females and spent longer durations on spawning shoals over the course of the spawning season (Martin and Olver, 1980; Miller and Kennedy, 1948; Muir et al., 2012; Royce, 1951). Males formed greater than four times as many spawning clusters and visited more sites than females. Spawning clusters were predominantly formed at night but were also observed during daylight hours, especially during the peak-spawning season. Although daily travel distances were similar between sexes, higher activity rates and longer periods spent on spawning shoals by males suggest that males may exert more energy than females during the spawning season. Overall, females performed more linear

movements over the course of the spawning season suggesting searching behaviour, while males were less persistent and more random in their movements.

Suitable spawning habitat was found to be abundant and widespread in Alexie Lake (Chapter 2), so it was not surprising that spawning clusters were also found dispersed throughout the entire nearshore region of Alexie Lake. Individual lake trout spawning site use widely varied in area (0.01–1.9 km²), with males visiting more than twice as many sites as females. The area of spawning site use was not found to differ between males and females in spite of greater visitation of spawning sites by males. Further, no individual lake trout visited all spawning sites or formed spawning clusters over the full extent of the collective lake trout spawning area (4.2 km²), suggesting individual lake trout utilize a subset of all possible spawning shoals over the duration of the spawning season. Whether this is a function of territories that individuals stay within (although no evidence has been found to date in other lake trout populations; Muir et al., 2012) or, more likely, the result of lake trout selecting spawning shoals with preferred environmental conditions (i.e. wind events; Martin and Olver, 1980; Muir et al., 2012), or mates (see Binder et al., 2015; Buchinger et al., 2015) is unknown and requires further investigation. In Chapter 2, I found that high variability in wind direction within and across spawning seasons suggests wind, and the resulting wave induced currents, are not predictable during the lake trout spawning season. This unpredictability in wind and the abundance of suitable habitat may favour spawning across multiple sites by lake trout as part of a bet-hedging strategy (Chapter 2; Fitzsimons and Marsden, 2014). Diversifying the spatial, physical, and chemical characteristics of spawning habitat, to increase the

overall portfolio performance of reproductive success (Moore et al., 2010) may be a productive tactic to buffer the unpredictable nature of wind and weather conditions.

Consistent with patterns revealed in previous studies, males formed spawning clusters earlier than females and spent longer durations on spawning shoals over the course of the spawning season (Martin and Olver, 1980; Miller and Kennedy, 1948; Muir et al., 2012; Royce, 1951). Males formed over four times as many spawning clusters and visited twice as many sites than females. These data support the hypothesis that males maximize reproductive fitness by spending as much time as possible on spawning shoals, thus maximizing possible mate encounters and fertilizations (Muir et al., 2012). Another explanation for the early arrival of males on spawning grounds is for signaling and attracting females (Esteve et al., 2008; Gunn, 1995; Muir et al., 2012). Recently, it has been suggested that males use display courtship behaviour such as “finning” in Great Bear Lake (Muir et al., 2012) or tactile courtship behaviour “hovering” in Lake Huron (Binder et al., 2015). Both behaviours involve small groups of males performing display behaviour to attract females with the commonality that both of these behaviours occur at the outer edge of the spawning shoal. Further, Buchinger et al., (2015) has found evidence that both spawning males and females are attracted to spawning male chemical cue. These results suggest part of the male reproductive strategy is to not only remain on active spawning shoals but also attract females to the spawning shoals it occupies; how exactly this is accomplished (visual display, chemical cue or both) requires further study.

Lake trout migration onto spawning shoals coincided with surface temperatures of ~15°C. The thermal preference of lake trout is between 5 °–15 °C (Plumb and Blanchfield, 2009), therefore migration onto spawning shoals and the onset of spawning

appears to be strongly regulated by thermal access to spawning habitat. In 2013, spawning onset began on August 29 and lasted over a 55 day period, concluding on October 23 when surface water temperature had declined to 5.5 °C. The length of the 2013 spawning period in Alexie Lake is quite long in comparison to other systems, where spawning typically lasts <14 d (Martin and Olver, 1980), although peak spawn duration (10 d) fell within this range. Lake trout predominantly spawned at night, typically around 22:30, but spawning also occurred throughout the day, especially during the peak season. This finding is consistent with an increasing number of studies showing that lake trout do not only spawn at night and that day spawning does occur and may not be as rare as once believed (Binder et al., 2015; Esteve et al., 2008; Muir et al., 2012).

Female lake trout invest large amounts of energy into their eggs, thus selecting high quality habitat and/or mates should be a priority. In contrast, males invest less energy than females in their gametes, thus energy should be put towards maximizing mating events by finding and remaining on active spawning shoals (Muir et al., 2012). I found supporting evidence for this with males expending greater energy on average than females over the course of the spawning season. This higher energy expenditure for males was in spite of travelling similar daily distances as females. The discrepancy in energy output is likely due to males increased frequency and duration on spawning shoals. Thus it appears that the disparity in gamete investment, where males invest less energy in gamete production, results in males having more energy to expend in attaining mates and egg fertilizations.

Female lake trout displayed greater linearity in movements than males over the course of the spawning season, which appears to be more energetically efficient than

non-linear movements typical of male fish. I interpret the increased linearity as the result of a female search strategy for mates and/or spawning habitat (Laidre et al., 2012). Thus, when ready to spawn, a female will move in a linear fashion searching for a spawning site with preferred environmental conditions, mates or both; while males wait on spawning shoals for females to arrive. Females also visited fewer sites than males, which could indicate that females have stricter requirements for spawning site selection than males; or, simply a byproduct of shorter duration on spawning shoals.

Although agonistic behaviour has not been observed in lake trout, evolutionary theory predicts male-male competition for mates should occur, especially when sex ratios are skewed towards males (Clutton-Brock and Parker, 1992), as is the case in lake trout (Binder et al., 2015; Martin and Olver, 1980; Muir et al., 2012). During spawning events, several males will travel with a female (Esteve et al. 2008; D. Callaghan personal observation). Typically, males will travel on one side of a female while jockeying for position next to her, even when the other side of the female remains unoccupied by other males (Binder et al., 2015). Binder et al. (2015) suggest that jockeying is likely a form of competition where the most fit individual remains in closest proximity to the female. Closer proximity has been shown to result in a greater proportion of fertilized eggs in other salmonine species (Blanchfield et al., 2003; Mjølnerød et al., 1998). This form of endurance competition by males may also explain why they have greater activity rates than females. Even though both sexes participate in the same spawning behaviours (i.e. travelling, sinking, and gamete release; Esteve et al., 2008), males remain on spawning shoals for a longer duration than females and therefore perform greater frequencies of these spawning behaviours.

The deviation from the general salmonine redd building strategy to an itinerant strategy may be a reflection of the predictability of habitat quality. Mating system theory predicts that when there is no parental care, female reproductive success is driven by habitat and mate quality, whereas male reproductive success is driven by spawning frequency (de Gaudemar, 1998). Habitat quality in salmonine systems is defined by water currents at redd sites (Chapman, 1988), with females fighting for territories with high quality redd sites and males competing for proximity to females (Esteve, 2005). In lakes, wave induced currents are believed to represent lake trout habitat quality in the absence of predictable current flow (i.e. river or groundwater inflow), although little quantitative evidence supports this (Fitzsimons and Marsden, 2014; Marsden et al., 1995; Martin and Olver, 1980). The lack of evidence may be due to winds unpredictability within and among spawning seasons (Chapter 2). Thus, instead of investing energy in building a redd on a site with unpredictable habitat quality, lake trout appear favour a bet-hedging strategy; increasing overall reproductive success by spawning at several sites with suitable substrate but unknown and varying habitat quality.

Chapter 4: Conclusions

The overall goal of my thesis research was to investigate lake trout reproduction in a northern lake. Much of what we know is from the southern extent of the lake trout's range, leaving a disconcerting knowledge gap on lake trout reproduction in northern boreal lakes. Chapter 2 focused on lake trout spawning habitat and correlates of embryonic survival. I assessed whether lake trout spawning habitat, typically characterized as wave-swept shoals with clean cobble that face predominant wind directions, is similar for a northern lake. Specifically, I tested if physical habitat and wind exposure were important determinants of spawning site use and embryonic survival. In Chapter 3, I compared reproductive strategies inferred from movement of males and females. I determined when and where lake trout spawn in a typical northern boreal lake; described sex-specific timing and movements of lake trout over the duration of a spawning season; and tested whether male and female lake trout employ a bet-hedging strategy. These two chapters are linked through the common thread of reproductive success and how habitat affects embryonic survival, reproductive strategies affect spawning behaviour, and how habitat and strategies form the lake trout mating system.

In Chapter 2, I found suitable lake trout spawning substrate in Alexie Lake to be widespread (virtually around the entire lake), while wind direction was unpredictable within and among spawning seasons. Lake trout spawning habitat has long been characterized as wave-swept shoals containing clean cobble that face predominant autumn wind directions; I found only partial support for this characterization in Alexie Lake. Spawning occurred in ~2 m water depth, on 3–15 cm diameter clean substrate

found on the leading edge of shoals that ended in a rock crib rising abruptly in nearshore regions around the lake. Lake trout spawning sites were widely distributed in Alexie Lake, and not limited to shoals facing a predominant wind direction (west). High variation in embryonic survival among lake trout spawning sites was observed, suggesting that a large gradient in habitat quality exists within a given lake. I developed a wind exposure model that incorporated wind, fetch and bathymetric slope to determine wind exposure at a suite of spawning sites. Modelled wind exposure did not predict embryonic survival, nor did physical habitat characteristics that may influence interstitial water flow on spawning shoals such as slope, depth, substrate length, or substrate shape. My findings challenge the conventional role of wind as a predominant predictor of lake trout spawning site quality. I propose that the unpredictable nature of wind and abundance of suitable habitat may favour lake-wide spawning by lake trout as a bet-hedging strategy in northern lakes.

In Chapter 3, I provide a detailed description of the lake trout mating system at the whole lake scale in a northern boreal lake, located in the core of the lake trout range with typical lake trout lake characteristics. Using data collected from a whole-lake acoustic telemetry array and filtered through a novel spatial temporal clustering analysis, I provide a detailed description of five male and six female lake trout movements over the course of the 2013 spawning season. Lake trout were found to cluster on spawning shoals throughout the entire nearshore region of Alexie Lake, as well as around several islands, which is consistent with Chapter 2 findings that suitable spawning habitat is abundant in Alexie Lake. The majority of spawning occurred over the duration of September in Alexie Lake (62.7 N), which is later than higher latitude lake trout spawning in Great

Bear Lake, NWT (mid-August; 65.3 N) and earlier than lower latitude spawning in the Laurentian Great Lakes (November, 43.7 N; Muir et al. 2012). My study population displayed spawning behaviour consistent with that of other studies; males arrived earlier than females and spent longer durations on spawning shoals over the course of the spawning season (Martin and Olver, 1980; Miller and Kennedy, 1948; Muir et al., 2012; Royce, 1951). Males formed more spawning clusters, visited more sites and spent a longer duration on spawning shoals than females. Also consistent with other studies, spawning was found to occur predominantly during night hours but was also observed during daylight hours, especially during the peak spawning season (Binder et al., 2015; Esteve et al., 2008; Muir et al., 2012). Males were found to have greater activity rates than females over the course of the spawning season. Although daily travel distances were similar between sexes, higher activity rates and longer durations spent on spawning shoals by males suggests that a male's reproductive strategy requires a higher activity rate than females. Overall, females performed more linear movements over the course of the spawning season suggesting searching behaviour, while males were less persistent and more random in their movements likely due to males patrolling spawning shoals. These data provide new insight into the reproductive strategies of male and female lake trout and further our knowledge on spawning site use for managing this iconic Canadian fish species.

My thesis broadens our understanding of the northern lake trout mating system and helps fill the knowledge gap required to manage this important northern species. I provide a qualitative and quantitative description of the 'rock crib' lake trout spawning habitat that has not been described previously. This data can help resource managers

replace or rehabilitate lake trout spawning sites impacted by development. My thesis also challenges conventional wisdom of the role of wind in lake trout spawning. Spawning shoals in Alexie Lake faced several different directions rather than just the predominant wind direction, while wind-induced currents did not predict habitat quality. Thus, a collection of spawning shoals facing different directions appears to be required to maintain a functioning northern lake trout mating system. My telemetry data revealed that lake trout move among multiple spawning sites over the course of the spawning season. Thus, managers should ensure that suitable lake trout spawning habitat is located ideally less than 0.5 km apart to allow for multiple site use. Lastly, my data showed that the majority of lake trout spawning occurred over the duration of September. A reduction in nearshore activity during the spawning season and the avoidance of all activity during peak spawning would reduce potential negative impacts of development to lake trout. The timing of spawning will differ with latitude (earlier in higher latitudes and later at lower latitudes) therefore lake trout spawning data from the lake in question or nearby lakes should be used to determine when spawning occurs. The methodological approaches used in this thesis for characterizing spawning habitat and behaviour can be utilized in future research of other economically, recreationally and culturally important fish species to ensure we conserve and sustain fisheries and fish species diversity, especially in Canada's North.

Literature Cited

- Allen, J.D., Walker, G.K., Adams, J.V., Jerrine Nichols, S., Edsall, C.C., 2005. Embryonic developmental progression in lake trout (*Salvelinus namaycush*)(Walbaum, 1792) and its relation to lake temperature. *Journal of Great Lakes Research* 31, 187–209.
- Andersson, M.B., 1994. *Sexual Selection*. Princeton University Press, Princeton.
- Bateman, A.J., 1948. Intra-sexual selection in drosophila. *Heredity* 2, 349–368.
- Becker, C.D., Neitzel, D.A., 1985. Assessment of intergravel conditions influencing egg and alevin survival during salmonid redd dewatering. *Environmental Biology of Fishes* 12, 33–46.
- Benaglia, T., Chauveau, D., Hunter, D.R., Young, D., 2009. mixtools: An R package for analyzing finite mixture models. *Journal of Statistical Software* 32, 1–29.
- Bengtsson, L., 1996. Mixing in ice-covered lakes. *Hydrobiologia* 322, 91–97.
- Berglund, A., 1997. Mating systems and sex allocation, in: Godin, J.-G.J. (Ed.), *Behavioural Ecology of Teleost Fishes*. Oxford University Press, Oxford, pp. 237–265.
- Bigelow, P.E., 2009. Predicting areas of lake trout spawning habitat within Yellowstone Lake, Wyoming (Ph.D. thesis). University of Wyoming, Laramie, WY.
- Binder, T.R., Thompson, H.T., Muir, A.M., Riley, S.C., Marsden, J.E., Bronte, C.R., Krueger, C.C., 2015. New insight into the spawning behavior of lake trout, *Salvelinus namaycush*, from a recovering population in the Laurentian Great Lakes. *Environmental Biology of Fishes* 98, 173–181.

- Birant, D., Kut, A., 2007. ST-DBSCAN: An algorithm for clustering spatialtemporal data. *Data & Knowledge Engineering* 60, 208–221.
- Bivand, R., Lewin-Koh, N., 2015. Maptools: Tools for reading and handling spatial objects.
- Blanchfield, P.J., Ridgway, M.S., 2005. The relative influence of breeding competition and habitat quality on female reproductive success in lacustrine brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 62, 2694–2705.
- Blanchfield, P.J., Ridgway, M.S., Wilson, C.C., 2003. Breeding success of male brook trout (*Salvelinus fontinalis*) in the wild. *Molecular Ecology* 12, 2417–2428.
- Blott, S.J., Pye, K., 2008. Particle shape: A review and new methods of characterization and classification. *Sedimentology* 55, 31–63.
- Blumer, L.S., 1982. A bibliography and categorization of bony fishes exhibiting parental care. *Zoological Journal of the Linnean Society* 75, 1–22.
- Buchinger, T.J., Li, W., Johnson, N.S., 2015. Behavioral evidence for a role of chemoreception during reproduction in lake trout. *Can. J. Fish. Aquat. Sci.* 1–6.
- Calenge, C., 2006. The package adehabitat for the R software: Tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197, 1035.
- Chapman, D.W., 1988. Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society* 117, 1–21.
- Claramunt, R.M., Jonas, J.L., Fitzsimons, J.D., Marsden, J.E., 2005. Influences of spawning habitat characteristics and interstitial predators on lake trout egg

- deposition and mortality. *Transactions of the American Fisheries Society* 134, 1048–1057.
- Clutton-Brock, T.H., Parker, G.A., 1992. Potential reproductive rates and the operation of sexual selection. *The Quarterly Review of Biology* 67, 437–456.
- Cott, P.A., Guzzo, M.M., Chapelsky, A.J., Milne, S.W., Blanchfield, P.J., 2015b. Diel bank migration of burbot (*Lota lota*). *Hydrobiologia* 757, 3–20.
- Cott, P.A., Johnston, T.A., Gunn, J.M., 2011. Food web position of burbot relative to lake trout, northern pike, and lake whitefish in four sub-Arctic boreal lakes: Food web position of burbot. *Journal of Applied Ichthyology* 27, 49–56.
- Cott, P.A., Schein, A., Hanna, B.W., Johnston, T.A., MacDonald, D.D., Gunn, J.M., 2015a. Implications of linear developments on northern fishes. *Environmental Reviews* 23, 177–190.
- Cott, P.A., Sibley, P.K., Somers, W.M., Lilly, M.R., Gordon, A.M., 2008. A review of water level fluctuations on aquatic biota with an emphasis on fishes in ice-covered lakes. *Journal of the American Water Resources Association* 44, 343–359.
- Crespi, B.J., Teo, R., 2002. Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. *Evolution* 56, 1008–1020.
- de Gaudemar, B., 1998. Sexual selection and breeding patterns: Insights from salmonids (Salmonidae). *Acta Biotheoretica* 46, 235–251.
- Deroche, S.E., 1969. Observations on the spawning habits and early life of lake trout. *The Progressive Fish-Culturist* 31, 109–113.

- Dugatkin, L.A., FitzGerald, G.J., 1997. Sexual selection, in: Godin, J.-G.J. (Ed.), Behavioural Ecology of Teleost Fishes. Oxford University Press, Oxford, pp. 266–291.
- Duguay, C.R., Flato, G.M., Jeffries, M.O., Ménard, P., Morris, K., Rouse, W.R., 2003. Ice-cover variability on shallow lakes at high latitudes: Model simulations and observations. Hydrological Processes 17, 3465–3483.
- Emlen, S.T., Oring, L.W., 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197, 215–223.
- Eschmeyer, P.H., 1964. The lake trout, *Salvelinus namaycush* (No. FL - 555). United States Geological Survey.
- Eschmeyer, P.H., 1955. The reproduction of lake trout in southern Lake Superior. Transactions of the American Fisheries Society 84, 47–74.
- Eshenroder, R.L., Bronte, C.R., Peck, J.W., 1995. Comparison of lake trout-egg survival at inshore and offshore and shallow-water and deepwater sites in Lake Superior. Journal of Great Lakes Research 21, Supplement 1, 313–322.
- Ester, M., Kriegel, H., S, J., Xu, X., 1996. A density-based algorithm for discovering clusters in large spatial databases with noise, in: Proceedings of Second International Conference on Knowledge Discovery and Data Mining. Portland, OR, pp. 226–231.
- Esteve, M., 2005. Observations of spawning behaviour in Salmoninae: *Salmo*, *Oncorhynchus* and *Salvelinus*. Reviews in Fish Biology and Fisheries 15, 1–21.

- Esteve, M., McLennan, D.A., Gunn, J.M., 2008. Lake trout (*Salvelinus namaycush*) spawning behaviour: The evolution of a new female strategy. *Environmental Biology of Fishes* 83, 69–76.
- Fisher, R.A., 1958. *The Genetical Theory of Natural Selection*. New York, Dover Publications.
- Fitzsimons, J.D., 1995. Assessment of lake trout spawning habitat and egg deposition and survival in Lake Ontario. *Journal of Great Lakes Research* 21, Supplement 1, 337–347.
- Fitzsimons, J.D., Marsden, J.E., 2014. Relationship between lake trout spawning, embryonic survival, and currents: A case of bet hedging in the face of environmental stochasticity? *Journal of Great Lakes Research* 40, 92–101.
- Flavelle, L.S., Ridgway, M.S., Middel, T.A., McKinley, R.S., 2002. Integration of acoustic telemetry and GIS to identify potential spawning areas for lake trout (*Salvelinus namaycush*). *Hydrobiologia* 483, 137–146.
- Fleming, I.A., 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 59–76.
- Fleming, I.A., 1996. Reproductive strategies of Atlantic salmon: Ecology and evolution. *Reviews in Fish Biology and Fisheries* 6, 379–416.
- Fleming, I.A., Gross, M.R., 1994. Breeding Competition in a Pacific Salmon (Coho: *Oncorhynchus kisutch*): Measures of Natural and Sexual Selection. *Evolution* 48, 637–657.

- Font, L.C., 2015. Behavioural Ecology of lake trout: From movement ecology to bioenergetics (PhD thesis). University of Toronto.
- Garant, D., Dodson, J.J., Bernatchez, L., 2001. A genetic evaluation of mating system and determinants of individual reproductive success in Atlantic salmon (*Salmo salar* L.). *Journal of Heredity* 92, 137–145.
- Groot, C., Margolis, L., 1991. Pacific Salmon Life Histories. UBC Press.
- Gross, M.R., 1996. Alternative reproductive strategies and tactics: Diversity within sexes. *Trends in Ecology & Evolution* 11, 92–98.
- Gross, M.R., 1985. Disruptive selection for alternative life histories in salmon. *Nature* 313, 47–48.
- Gross, M.R., 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes, in: Wootton, R., Potts, G. (Eds.), *Fish Reproduction : Strategies and Tactics*. Academic Press, London, pp. 55–75.
- Gunn, J., Steedman, R.J., Ryder, R., 2004. Boreal Shield Watersheds: Lake Trout Ecosystems in a Changing Environment. CRC Press, Lewis Publishing, Boca Raton, Florida.
- Gunn, J.M., 1995. Spawning behavior of lake trout: Effects on colonization ability. *Journal of Great Lakes Research* 21, Supplement 1, 323–329.
- Guzzo, M.M., Blanchfield, P.J., Chapelsky, A.J., Cott, P.A., 2015. Resource partitioning among top-level piscivores in a sub-Arctic lake during thermal stratification. *Journal of Great Lakes Research*.

- Hafner, W.D., Hites, R.A., 2005. Effects of wind and air trajectory directions on atmospheric concentrations of persistent organic pollutants near the Great Lakes. *Environmental Science & Technology* 39, 7817–7825.
- Hallermeier, R.J., 1981. Critical wave conditions for sand motion initiation (Coastal Engineering Technical Aid No. 81-10). United States Army Corps of Engineers Coastal Engineering Resource Center, Fort Belvoir, VA.
- Healey, M.C., Prince, A., 1998. Alternative tactics in the breeding behaviour of male coho salmon. *Behaviour* 135, 1099–1124.
- Healey, M.C., Woodall, W.L., 1973. Experimental cropping of lakes: II. Physical and chemical features of the lakes. Fisheries Research Board of Canada Technical Report 348, 1-19.
- Horns, W.H., 1985. Differences in early development among lake trout (*Salvelinus namaycush*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* 42, 737–743.
- Janssen, J., Jude, D.J., Edsall, T.A., Paddock, R.W., Watrus, N., Toney, M., Mckee, P., 2006. Evidence of lake trout reproduction at Lake Michigan's mid-lake reef complex. *Journal of Great Lakes Research* 32, 749–763.
- Jonsson, B., Jonsson, N., 1993. Partial migration: Niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* 3, 348–365.
- Keenleyside, M.H., Dupuis, H.M., 1988. Courtship and spawning competition in pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Zoology* 66, 262–265.
- Kenney, B.C., 1996. Physical limnological processes under ice. *Hydrobiologia* 322, 85–90.

- Koçak, K., 2008. Practical ways of evaluating wind speed persistence. *Energy* 33, 65–70.
- Kokko, H., Jennions, M.D., 2008. Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology* 21, 919–948.
- Koseki, Y., Maekawa, K., 2000. Sexual selection on mature male parr of masu salmon (*Oncorhynchus masou*): Does sneaking behavior favor small body size and less-developed sexual characters? *Behavioral Ecology and Sociobiology* 48, 211–217.
- Laidre, K.L., Born, E.W., Gurarie, E., Wiig, O., Dietz, R., Stern, H., 2012. Females roam while males patrol: Divergence in breeding season movements of pack-ice polar bears (*Ursus maritimus*). *Proceedings of the Royal Society B: Biological Sciences* 280: 20122371.
- MacLean, J.A., Evans, D.O., Martin, N.V., DesJardine, R.L., 1981. Survival, growth, spawning distribution, and movements of introduced and native lake trout (*Salvelinus namaycush*) in two inland Ontario lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 1685–1700.
- Malm, J., Bengtsson, L., Terzhevik, A., Boyarinov, P., Glinsky, A., Palshin, N., Petrov, M., 1998. Field study on currents in a shallow, ice-covered lake. *Limnology and Oceanography* 43, 1669–1679.
- Manny, B.A., Edsall, T.A., Peck, J.W., Kennedy, G.W., Frank, A.M., 1995. Survival of lake trout eggs on reputed spawning grounds in Lakes Huron and Superior: *in situ* incubation, 1987-1988. *Journal of Great Lakes Research* 21, 302–312.
- Markfort, C.D., Perez, A.L.S., Thill, J.W., Jaster, D.A., Porté-Agel, F., Stefan, H.G., 2010. Wind sheltering of a lake by a tree canopy. *Water Resources Research* 46, W03530.

- Marsden, J.E., Ellrott, B.J., Claramunt, R.M., Jonas, J.L., Fitzsimons, J.D., 2005. A comparison of lake trout spawning, fry emergence, and habitat use in lakes Michigan, Huron, and Champlain. *Journal of Great Lakes Research* 31, 492–508.
- Marsden, J.E., Perkins, D.L., Krueger, C.C., 1995. Recognition of spawning areas by lake trout: Deposition and survival of eggs on small, man-made rock piles. *Journal of Great Lakes Research* 21, 330–336.
- Martin, N.V., 1957. Reproduction of lake trout in Algonquin Park, Ontario. *Transactions of the American Fisheries Society* 86, 231–244.
- Martin, N.V., Olver, C.H., 1980. The lake charr, *Salvelinus namaycush*, in: Balon, E.K. (Ed.), *Charrs: Salmonid Fishes of the Genus Salvelinus*, Perspectives in Vertebrate Science. Dr. LW Junk Publishers, The Hague, The Netherlands, pp. 205–277.
- McAughey, S.C., Gunn, J.M., 1995. The behavioral response of lake trout to a loss of traditional spawning sites. *Journal of Great Lakes Research* 21, Supplement 1, 375–383.
- Merriman, D., 1935. Squam lake trout. *Bulletin of the Boston Society of Natural History*. 75, 3–10.
- Miller, R.B., Kennedy, W.A., 1948. Observations on the lake trout of Great Bear Lake. *Journal of the Fisheries Research Board of Canada* 7b, 176–189.
- Mjølnerød, I.B., Fleming, I.A., Refseth, U.H., Hindar, K., 1998. Mate and sperm competition during multiple-male spawnings of Atlantic salmon. *Canadian Journal of Zoology* 76, 70–75.

- Moore, J.W., McClure, M., Rogers, L.A., Schindler, D.E., 2010. Synchronization and portfolio performance of threatened salmon. *Conservation Letters* 3, 340–348.
- Morbey, Y., 2000. Protandry in Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 1252–1257.
- Muir, A.M., Blackie, C.T., Marsden, J.E., Krueger, C.C., 2012. Lake charr *Salvelinus namaycush* spawning behaviour: New field observations and a review of current knowledge. *Reviews in Fish Biology and Fisheries* 22, 575–593.
- Perkins, D.L., Krueger, C.C., 1995. Dynamics of reproduction by hatchery-origin lake trout (*Salvelinus namaycush*) at Stony Island Reef, Lake Ontario. *Journal of Great Lakes Research* 21, Supplement 1, 400–417.
- Plumb, J.M., Blanchfield, P.J., 2009. Performance of temperature and dissolved oxygen criteria to predict habitat use by lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences* 66, 2011–2023.
- Podsetchine, V., Schernewski, G., 1999. The influence of spatial wind inhomogeneity on flow patterns in a small lake. *Water Research* 33, 3348–3356.
- Quesada, A., Vincent, W.F., Kaup, E., Hobbie, J.E., Laurion, I., Pienitz, R., López-Martínez, J., Durán, J.-J., 2006. Landscape control of high latitude lakes in a changing climate, in: Bergstrom, D.M., Convey, P., Huiskes, A.H.L. (Eds.), *Trends in Antarctic Terrestrial and Limnetic Ecosystems*. Springer Netherlands, pp. 221–252.
- Quinn, T.P., Foote, C.J., 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon, *Oncorhynchus nerka*. *Animal Behaviour* 48, 751–761.

- R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Redick, R.R., 1967. A review of literature on lake trout life history with notes on Alaskan management. Alaska Department of Fish; Game, Division of Sport Fish.
- Revelle, W., 2015. Psych: Procedures for psychological, psychometric, and personality research. Northwestern University, Evanston, Illinois.
- Rhéaume, G., Caron-Vuotari, M., 2013. The Future of Mining in Canada's North. The Conference Board of Canada, Ottawa, Ontario.
- Riley, S.C., Binder, T.R., Wattrus, N.J., Faust, M.D., Janssen, J., Menzies, J., Marsden, J.E., Ebener, M.P., Bronte, C.R., He, J.X., Tucker, T.R., Hansen, M.J., Thompson, H.T., Muir, A.M., Krueger, C.C., 2014. Lake trout in northern Lake Huron spawn on submerged drumlins. *Journal of Great Lakes Research* 40, 415–420.
- Rowan, D.J., Kalff, J., Rasmussen, J.B., 1992. Estimating the mud deposition boundary depth in lakes from wave theory. *Canadian Journal of Fisheries and Aquatic Sciences* 49, 2490–2497.
- Royce, W.F., 1951. Breeding habits of lake trout in New York. *Fishery Bulletin of the Fish and Wildlife Service* 52, 39–76.
- Sawatzky, C., Michalak, D., Reist, J., Carmichael, T., Mandrak, N., Heuring, L., 2007. Distributions of freshwater and anadromous fishes from the mainland Northwest Territories, Canada. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* 2793, 239.

- Seibt, C., Peeters, F., Graf, M., Sprenger, M., Hofmann, H., 2013. Modeling wind waves and wave exposure of nearshore zones in medium-sized lakes. *Limnology and Oceanography* 58, 23–36.
- Sharma, S., Jackson, D.A., Minns, C.K., 2009. Quantifying the potential effects of climate change and the invasion of smallmouth bass on native lake trout populations across Canadian lakes. *Ecography* 32, 517–525.
- Sly, P.G., 1988. Interstitial water quality of lake trout spawning habitat. *Journal of Great Lakes Research* 14, 301–315.
- Smith, F., 2013. Understanding HPE in the VPS Telemetry System. VEMCO Tutorials. <http://vemco.com/wp-content/uploads/2013/09/understanding-hpe-vps.pdf>
- Trivers, R., 1972. Parental investment and sexual selection, in: Cambell, B. (Ed.), *Sexual Selection and the Descent of Man*. Aldine Press, Chicago, pp. 139–179.
- Vladykov, V.D., 1962. Osteological studies on Pacific salmon of the genus *Oncorhynchus*. *Fisheries Research Board Canada Bulletin* 136, 1–172.
- Wan, H., Wang, X.L., Swail, V.R., 2010. Homogenization and trend analysis of Canadian near-surface wind speeds. *Journal of Climate* 23, 1209–1225.
- Wantzen, K.M., Rothhaupt, K.-O., Mörtl, M., Cantonati, M., G.-Tóth, L., Fischer, P., 2008. Ecological effects of water-level fluctuations in lakes: An urgent issue. *Hydrobiologia* 613, 1–4.
- Wetzel, R.G., 2001. *Limnology: Lake and River Ecosystems*, 3rd ed. Elsevier, San Diego.
- Wilton, M.L., 1985. Water drawdown and its effects on lake trout (*Salvelinus namaycush*) reproduction in three south-central Ontario lakes. *Ontario Fisheries Technical Report Series No. 20*.

Zuur, A., Leno, E., Walker, N., Saveliev, A., Smith, G., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, New York, USA.

Appendix

The spatial positions of lake trout implanted with acoustic transmitters (30 V13P-1 L and 14 V13AP-1L, VEMCO Ltd., Bedford, NS), were determined using a VEMCO Positioning System (VPS; VEMCO Ltd.). VPS uses hyperbolic positioning, also known as multilateration, which measures the time difference on arrival (TDOA) of a signal from a transmitter at three or more time-synchronized receivers. An array of 72 underwater omni-directional acoustic receivers (VEMCO, VR2W) with a mean distance of 201.4 m (range: 120.4 – 311.9 m) between receivers, was deployed in Alexie Lake, NWT, to monitor spawning site selection and habitat use of 46 lake trout continuously from June 2012 to September 2014 (Fig. A.1). Synchronizing transmitters or “sync tags” (VEMCO, V16-1 L) with nominal code transmission delays of 1200 s (range: 1100 – 1300 s) were used to synchronize the internal clocks of receivers. Sync tags were attached to each receiver mooring 1 m above the receiver. An additional 11 sync tags were deployed and distributed throughout the array as reference tags to aid in system synchronization and positioning accuracy (Fig. A.1).

Animal tracking technologies (i.e. VPS) estimate positions with varying degrees of measurement error. It is important to detect and remove positions with excessive measurement error, while retaining positions within an acceptable range of measurement error appropriate for a specific data analysis (Meckley et al. 2014). I performed a spatial temporal cluster analysis using a density-based clustering algorithm ST-DBSCAN (*Spatial Temporal Density-Based Spatial Clustering of Applications with Noise*;



Figure A1 – VEMCO VR2W acoustic receiver and reference tag positions in Alexie Lake, NWT.

as per Birant and Kut, 2007) in order to determine where lake trout spawn. Following the approach proposed by Meckley et al. (2014) for filtering hyperbolically positioned underwater acoustic telemetry data, I establish data quality objectives for the spatial temporal clustering analysis. Lake trout are known to spawn in the nearshore region of Alexie Lake (See Chapter 2); therefore, I performed tag trials in the nearshore region to determine measurement error. Baseline system performance in terms of position measurement error was established both in the VPS array using sync tags, and outside of the array (nearshore) using stationary tag tests, as well as mobile tag test focusing on the nearshore region of Alexie Lake. The performance of the VPS array was tested using 2 V13-1P transmitters, which is the same transmitter model implanted in lake trout except the transmission rate is faster for the test tags to increase probability of detection (mean transmission rate = test tags 30 s vs. animal tags 120 s). Test tag transmitters were attached to an anchored buoy 0.5 m above the spawning shoal at mean depth of 1.9 m (range: 1.1 – 4.5 m). Buoys were submerged just below the water surface to ensure the anchor, tag and buoy were in vertical alignment. Stationary tags were left for mean 23.3 h (range: 16.1 - 47.8 h) in 2 different locations on each of 12 known spawning shoals distributed around the lake (Fig. A.2). During the spawning season, lake trout have been observed to move among spawning shoals (MacLean et al, 1981), often in the nearshore region (D. Callaghan personal observation). Therefore I designed a tag trial study to mimic nearshore movement of lake trout during spawning. The same 2 V13-1P transmitters from the stationary tests were also used in mobile tests comprising of 6 transects cumulatively following the entire shoreline and majority of island shorelines in Alexie Lake (Fig. A.3). The selected transmitter was suspended at 1.6 m below the



Figure A.2 – Stationary tag trial positions (red circles) in Alexie Lake, NWT, on 12 known spawning shoals

surface and fastened to a rope with attached downrigger in order to maintain vertical alignment. A GPS unit was fixed directly above the transmitter to monitor the transmitters true position. The GPS recorded real positions on average every 27.33 se (range: 1 – 43 s). The mobile tests were conducted at a mean speed of 0.63 m/s (range: 0 - 2.4 m/s) and mean time span of 2.2 h (range 1.5 – 2.7 h). GPS clocks were not synchronized with the acoustic receivers at the time of the test; in order to synchronize the times I followed Meckley et al. (2014) method to calculate and apply a constant time offset (3.5 s, see below) to the timestamps of the GPS positions to minimize error between the GPS track and the mobile track calculated by the VPS. Time error was reduced using the Optim function in R, which used the Broyden-Fletcher-Goldfarb-Shanno method (Nocedal and Wright, 2006). For each VPS fix, measurement error was calculated as Euclidean distance between real positions (x_{real}, y_{real}) and VPS calculated positions (x_{calc}, y_{calc}):

$$(1) \quad MeasurementError = \sqrt{(x_{calc} - x_{real})^2 + (y_{calc} - y_{real})^2}$$

Real positions for stationary tag trials were calculated as the median of four GPS points (two GPS positions taken at the start of the trial and two GPS positions taken at the end of the trial with two separate GPS units) to reduce potential GPS positioning error.

Spatial Error Evaluation

Horizontal positioning error (HPE) is unitless estimate of error sensitivity assigned by VEMCO to positions for both sync tags and animal-implanted tags. Auxiliary testing must be performed in order to discern what value of HPE can be used as a data



Figure A.3 – Mobile tag test in Alexie Lake, NWT. Each line colour represents a separate mobile trial. Filled circles represent the start position and filled squares represent at the finish position of each trial.

filter. HPE is the theoretical value based on the receiver array geometry as well as expected error due to the influence of environmental conditions (depth, temperature and salinity) on acoustics. If a relationship between HPE and measurement error for sync tags is representative of animal implanted tags then HPE value can be used as a confidence estimate for each fish position (Coates et al., 2013). I evaluated the HPE value provided for fish tags calculated by VEMCO using stationary tags on spawning shoals with known locations measured by a handheld GPS. There is no one number that can be calculated to characterize a VPS's accuracy, as accuracy depends on many factors that are variable over time and location; HPE and measured positioning error will likely have no relationship between one another (Smith, 2013). This is because HPE is not intended to predict what the error is equal to for a specific calculated position; instead, it is intended to predict the relative precision or spread of calculated positions that have that value of HPE (Smith, 2013). I therefore compared HPE and measured error statistically by calculating the 2DRMS (twice the distance root mean square) linear model as shown by Meckley et al., (2014). Due to the impact of very large measurement errors and very large HPE values on developing a linear relationship, both measurement error and HPE were truncated at 95 percentile, resulting in 92.8 % of the original dataset being retained. The measurement error in the x direction (X_e) and y direction (Y_e) were calculated as the Euclidean distance between real x and y and calculated x and y. I then binned measurement error (X_e , Y_e) by one unit of HPE, calculating 2DRMS (twice the distance root mean square) for each bin:

$$(2) \quad 2DRMS = 2 \sqrt{SD(X_e)^2 + SD(Y_e)^2}$$

A segmented relationship between the 2DRMS of binned HPE and measurement error was visually apparent after plotting the relationship; therefore, a breakpoint analysis was conducted to determine the breakpoints in the segmented regression (Fig. A.4). I only included data less than the first break point (HPE=107, retaining 76.4% of full dataset) in the linear model developed to determine a relationship between 2DRMS of binned HPE values and measurement error (Fig. A.5). Based on this relationship, I sequentially tested the clustering analysis under suite of HPE filters.

Spatial Temporal Cluster Analysis

I performed a spatial temporal cluster analysis using a density-based clustering algorithm ST-DBSCAN (Birant and Kut, 2007) to determine where lake trout spawn. The spatial temporal clustering algorithm requires data points with three required fields: x coordinate, y coordinate and timestamp. Additionally four parameters are required to create clusters: epsilon distance – the Euclidean distance parameter for spatial attributes; epsilon time – the Euclidean distance parameter for time attributes; minimum points – the minimum number of points required to create a cluster; and $\Delta\epsilon$ – the acceptable change in time between the current cluster mean and the potential new addition to the cluster.

Parameters were determined a simple heuristic suggested by Ester et al., (1996), which is effective at determining the both epsilon parameters and minimum points. First, minimum points $\approx \ln(n)$ where n is the size of the position data; epsilon must be picked depending on this minimum points value. Then the distances to the *k-nearest neighbours* must be determined for distance and time, where k is equal to minimum points. The *k-distance values* are then sorted in descending order and graphed (i.e. Fig. A.6). The

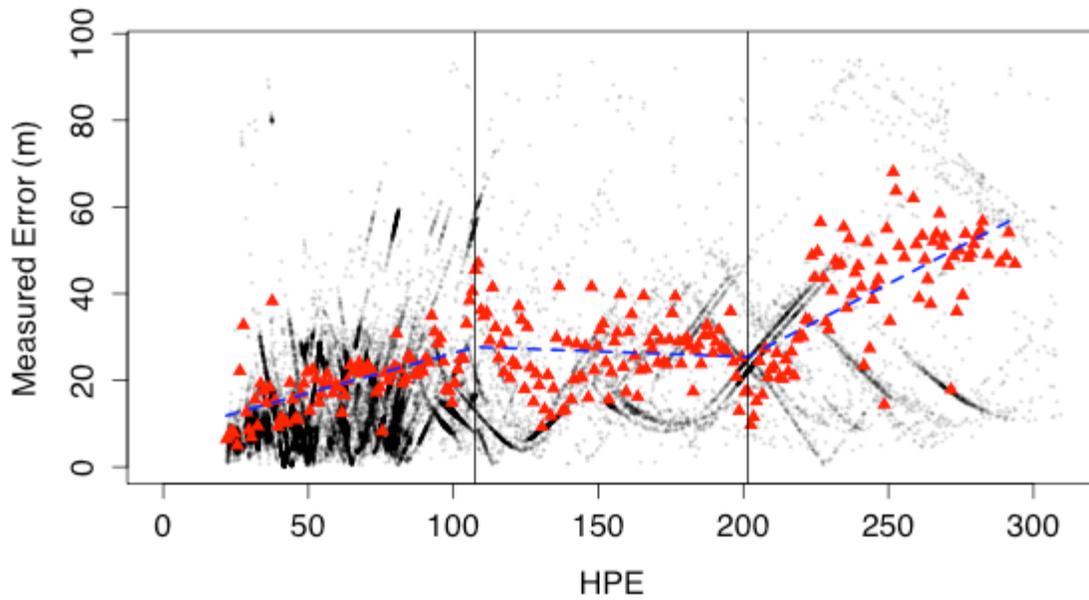


Figure A.4 – 2DRMS of binned HPE’s relationship to measurement error. Red triangles represent 2DRMS of binned HPE, black points represent data points, blue dashed line represents the segmented regression line, vertical black lines represent the breakpoints in the segmented regression.

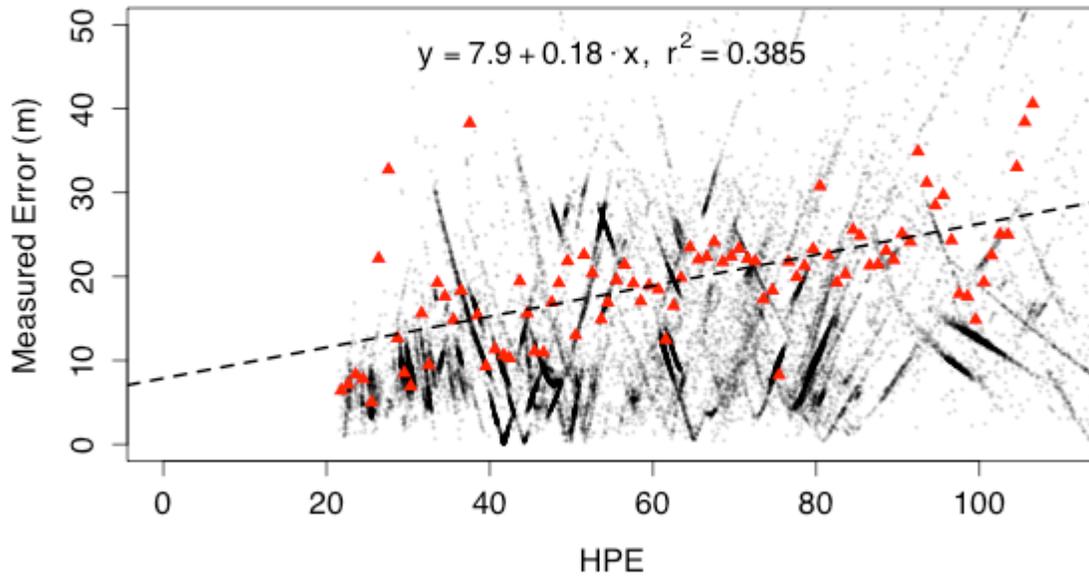


Figure A.5 – 2DRMS of binned HPE’s relationship to measurement error. Red triangles represent 2DRMS of binned HPE, black points represent data points, dashed line represents the linear model $y = 0.18x + 7.9$.

LT-31 K-Dist Space

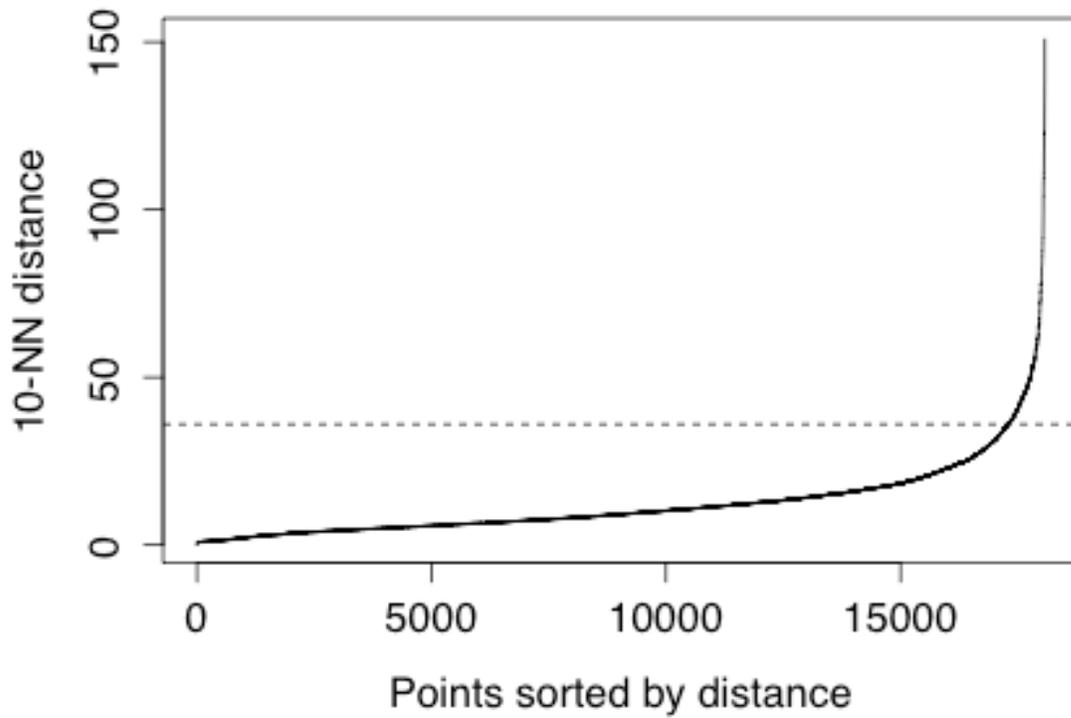


Figure A.6 – Example of a sorted k -distance plot for the 10th nearest neighbour. The solid line represents the data and the dashed line represents the parameter estimate

threshold point of the “elbow” in the sorted graph determines epsilon. The last parameter $\Delta\epsilon$ is more subjective for determining whether you want to be more inclusive, lower number of clusters, higher points per cluster or less inclusive higher number of clusters and lower points per cluster. I selected a $\Delta\epsilon$ of 2 standard deviations to be more inclusive. To test the cluster analysis performance under a suite of HPE filters and determine the maximum allowable error, I simulated movement tracks using a Lévy flight model — a special case of random walk — and performed the cluster analyses on the simulated track. The timestamp started at 0 for the first position and a random time interval selected from the fitted time interval distribution (log-normal) of the mobile tag trials was added to the proceeding simulated points. Next, I introduced error to the simulated or “real” track by randomly selecting an x and y error measurement from the fitted x (log-normal) and y (weibull) error distributions (i.e. Fig. A.7), produced from the mobile tag trials for each simulated position and reran the cluster analysis (i.e. Fig. A.8). This was systematically done including no HPE filter as well as 27m 2DRMS HPE filter to 15m 2DRMS HPE filter (95% confidence error < 27m to 15m) by 1 m 2DRMS bins derived from the linear modeled relationship between 2DRMS and HPE. For each HPE filter 100 error tracks were generated for each of the 100 simulated “real” tracks, totaling 10,000 error simulations. From these simulations, I calculated the mean ratio of error clusters to real clusters, the mean overlap of real clusters by error clusters, the mean percent of missed clusters defined as real clusters with no overlap by error clusters, mean percent of cluster overhang defined as percent area of error clusters that overhang the area of real clusters, and mean percent of phantom clusters defined as error clusters with no overlap of real clusters (summarized in Fig. A.9). The most dramatic changes are from no

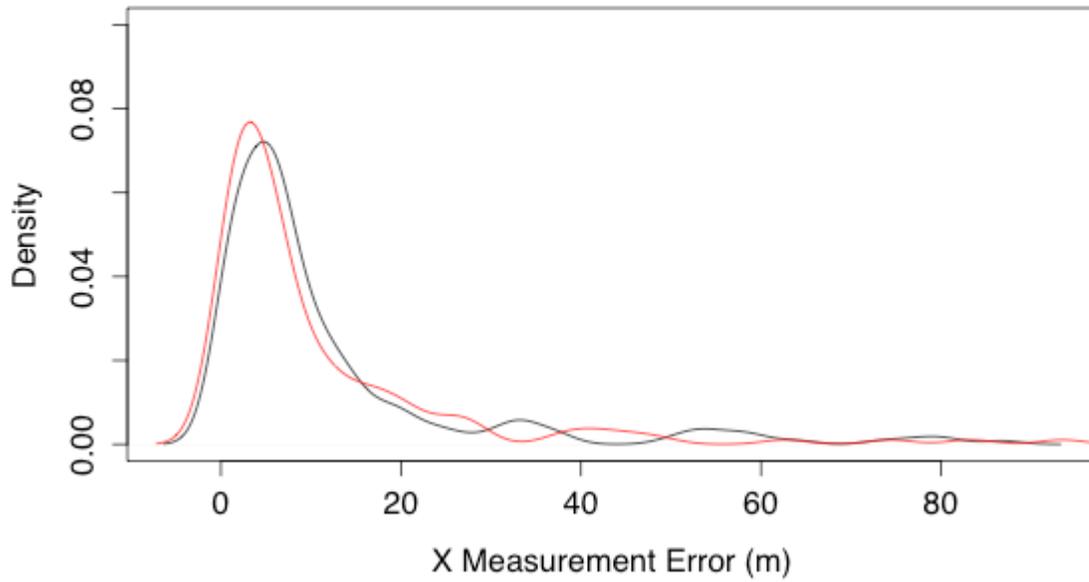


Figure A.7 – Kernel density estimate (black line) for measurement error of a mobile tag trial in the x coordinate. The red line represents the best fit distribution (log-normal) used to generate x measurement error in the simulations.

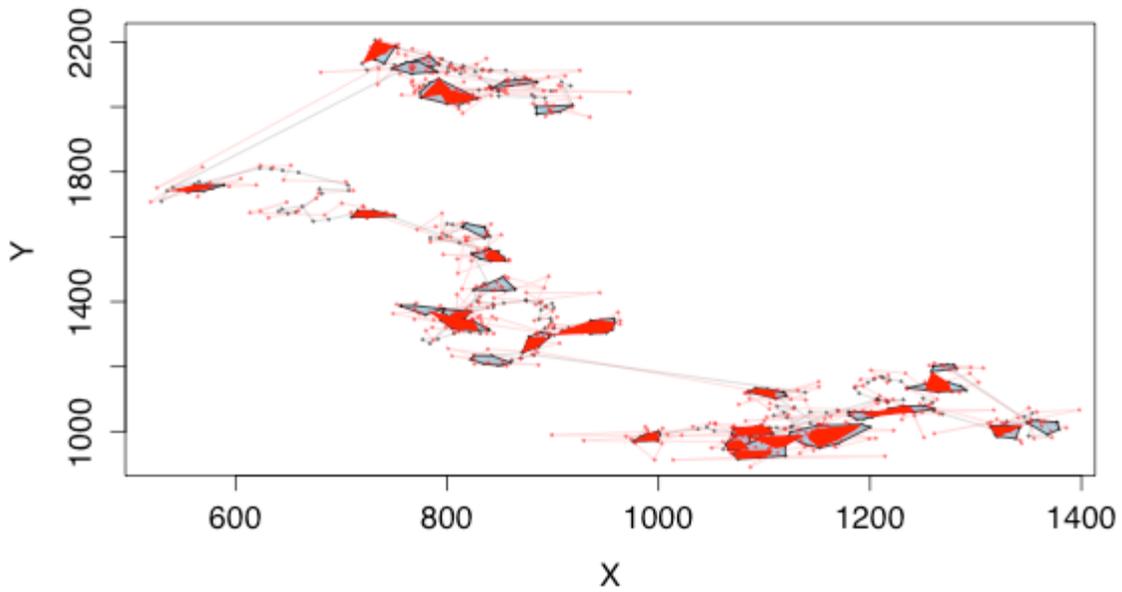


Figure A.8 – An example of overlap between error clusters (red) and real clusters (blue) of simulated tracks (black line and dots) after error is added to each point (red line and dots).

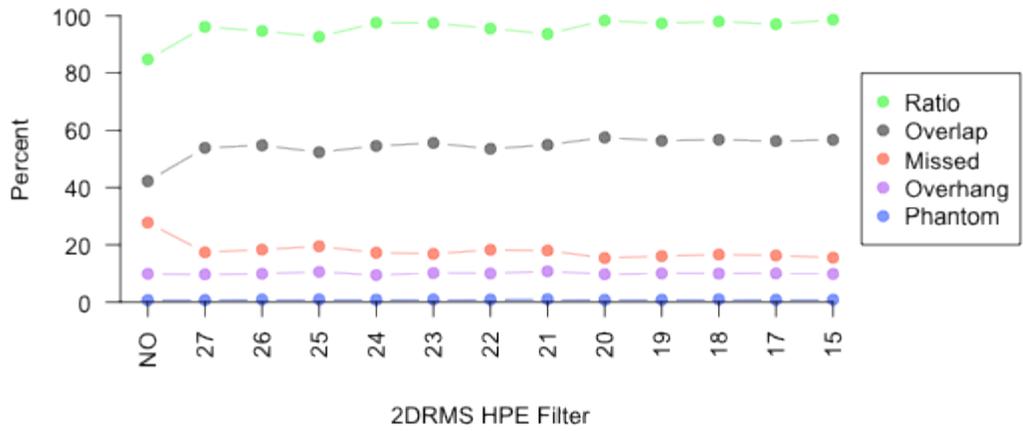


Figure A.9 – Summary graph of cluster simulations to determine the maximum allowable 2DRMS HPE filter for the cluster analysis. Ratio represents the mean ratio of error clusters to real clusters, Overlap represents the mean overlap of real clusters by error clusters, Missed represents the mean percent of real clusters with no overlap of error clusters, Overhang represents mean percent area of error clusters that overhang the area of real clusters, and Phantom represent mean percent of error clusters with no overlap of real clusters.

2DRMS HPE filter to 27 m 2DRMS HPE with a 11.4% increase in error to real cluster ratio, 10.1% increase in cluster overlap, and a 12.3% decrease in missed clusters, with similar values for cluster overhang and phantom clusters (Table A.1). Both figure A.9 and table A.1 show how little decreasing the HPE filter from 27 to 15 m 2DRMS affects the performance of the cluster analysis with 27 m 2DRMS HPE filter either performing optimally for missed, overhang phantom statistics, within 1 SD of the mean for ratio statistic and within 2 SD of mean overlap statistic. This is in contrast to when no HPE filter is applied, the performance is inferior to the mean by 10% in all statistics except overhang and phantom statistics, which remain virtually constant throughout the suite of filters. Please note that for each 2DRMS HPE filter simulation, 500 positions are always used, therefore the simulations do not take into account the loss of data that is incurred by filtering data by lower HPE values (increasing precision) which likely affects cluster formation, especially when filters create variable time gaps. Therefore, it appears that the 27 m 2DRMS HPE filter is an ideal choice for both cluster analysis performance and data retention.

Table A.1 – 2DRMS HPE filter summary statistics for cluster simulations to determine the maximum allowable 2DRMS HPE filter for the cluster analysis. The table showcases no HPE filter and 27 m 2DRMS HPE filter, as well as mean \pm SD and optimum values for 27 to 15 m 2DRMS HPE Filters. Ratio represents the mean ratio of error clusters to real clusters, Overlap represents the mean overlap of real clusters by error clusters, Missed represents the mean percent of real clusters with no overlap of error clusters, Overhang represents mean percent area of error clusters that overhang the area of real clusters, and Phantom represent mean percent of error clusters with no overlap of real clusters.

2DRMS HPE Filter	Ratio	Overlap	Missed	Overhang	Phantom
No	84.7 %	42.2 %	27.7 %	9.9 %	0.7 %
27	96.1 %	52.3 %	15.4 %	9.5 %	0.8 %
27-15 (Mean \pm SD)	96.4 \pm 1.9 %	55.3 \pm 1.5 %	17.1 \pm 1.2 %	10.0 \pm 0.4 %	0.9 \pm 0.1 %
27-15 (Optimum)	98.6 %	57.5 %	15.4 %	9.5 %	0.8 %

References

- Birant, D., Kut, A., 2007. ST-DBSCAN: An algorithm for clustering spatial–temporal data. *Data & Knowledge Engineering* 60, 208–221.
- Ester, M., Kriegel, H., S, J., Xu, X., 1996. A density-based algorithm for discovering clusters in large spatial databases with noise, in: *Proceedings of Second International Conference on Knowledge Discovery and Data Mining*. Portland, OR, pp. 226–231.
- Meckley, T.D., Holbrook, C.M., Wagner, C.M., Binder, T.R., 2014. An approach for filtering hyperbolically positioned underwater acoustic telemetry data with position precision estimates. *Animal Biotelemetry* 2, 1–13.
- MacLean, J.A., Evans, D.O., Martin, N.V., DesJardine, R.L., 1981. Survival, growth, spawning distribution, and movements of introduced and native lake trout (*Salvelinus namaycush*) in two inland Ontario lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 1685–1700.
- Nocedal, J., Wright, S., 2006. *Numerical Optimization*, 2nd ed, Springer Series in Operations Research and Financial Engineering. Springer New York.
- Smith, F., 2013. Understanding HPE in the VPS Telemetry System. VEMCO Tutorials. [<http://vemco.com/wp-content/uploads/2013/09/understanding-hpe-vps.pdf>]