

Salmonid Thermal Habitats in Lake Superior Tributaries

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Abstract

For some potamodromous salmonid species, such as the Brook Trout, streams are a critical spawning habitat but also habitat for juveniles and stream residents to grow. Salmonids are coldwater fishes and cooler stream water temperatures are essential for individuals to avoid temperature stress and in some cases death. My goal was to study relationships between salmonid relative abundance and stream thermal habitat characteristics observed at multiple spatial scales within Lake Superior tributary streams. These spatial scales included the microhabitat (~1 m²), reach (50 m) and segment (2 km) spatial scale. At the microhabitat scale, the ability of unbaited underwater cameras to obtain estimates of relative abundance comparable to the estimates of relative abundance obtained through electrofishing surveys was evaluated. The estimates of relative abundance obtained using visual surveys and electrofishing surveys were found to be comparable, and thus microhabitat relative abundance and reach catch-per-minute were the measurements of relative abundance used to study salmonid ecology at the three spatial scales. Results showed that salmonid relative abundance at the microhabitat scale was lower when surface water temperature was higher, higher when the temperature variation observed within a reach was higher and was higher stream segments had a higher density of predicted flow pathways. However, at all spatial scales, these temperature variables did not explain variations in salmonid relative abundance to the same degree as certain random variables such as stream, date and year sampled. Use of landscape spatial scale analyses generally performed well in locating areas of thermal refugia within a stream network. Most reaches containing predicted flow pathways exhibited a greater range in water temperatures than non-flow pathway reaches with multiple reaches contributing cold water to localized regions of a stream throughout the entire summer. Though patterns of salmonid distribution and abundance within a stream network cannot be solely explained using thermal habitat characteristics, sustainable land use practices that maintain the thermal integrity of streams should allow Lake Superior and its tributary streams to continue supporting healthy salmonid populations.

Lay Summary

Salmonids are a group of ray-finned fishes that live in aquatic ecosystems across the globe. In North America, Lake Superior and the streams that flow into Lake Superior (known as tributary streams) are home to multiple native and introduced salmonid species. For many Lake Superior salmonids, tributary streams are a critical spawning habitat where adult fish deposit their eggs. Once juvenile salmonids emerge from their eggs, they will occupy, forage and grow in their natal stream (or the stream where they were born). Some juvenile salmonids will grow quickly and eventually migrate into Lake Superior. Other juvenile salmonids will spend their entire lives in their natal stream. Lake Superior salmonids, such as the Brook Trout, are some of the most prized recreational fishes in Ontario. Brook Trout, as well as other salmonids, require cold-water habitats with lots of oxygen and are sensitive to ecological disturbances. Factors such as overfishing, loss of aquatic habitat, climate change and the introduction of invasive species all threaten the lives of Lake Superior salmonids. In recent years, many salmonid populations have declined or become completely removed from regions of Lake Superior. Salmonids are coldwater fishes and prolonged exposure to warm water temperatures can be deadly for individuals. Cold water temperatures and the availability of cold-water habitats are critical for salmonid survival especially during the summer months when stream surface water temperatures often reach lethal levels. My research aims to further our understanding of stream thermal habitats and salmonids use of thermal habitats. Results of my research show that stream water temperatures change daily, monthly and seasonally and the presence of salmonids within a given habitat is often more complicated than how much cold-water habitat is available. With that said, salmonid abundance (or the number of fish) was found to be higher in habitats with colder water temperatures. A better understanding of stream water temperatures and how salmonids use the cold-water habitats during the warm summer months is essential if we want to restore and protect Lake Superior salmonid populations and their stream habitats.

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Chapter 1. Introduction

1.1 Background

Traditional research methods used to study fishes have included angling, electrofishing, netting and the use of various piscicides. Past studies have shown these research methods have the potential to harm sampled fish (Elliot & Bagenal, 1972; Hudy, 1985; Frezza et al., 2003; Bartholomew & Bohnsack, 2005; Clearwater et al., 2008). Among these traditional methods, electrofishing is a very popular method used to sample fishes in both lakes and streams. Electrofishing units generate an electric current underwater which can immobilize nearby fish making them easier to catch. By incorporating multiple surveys (or passes) into an experimental design, researchers can obtain information concerning fish population and community structure within a given study area (Zippin, 1956; Frezza et al., 2003). Though generally considered to be a reliable method for studying fishes, past studies have shown electrofishing can cause immediate or delayed harm to shocked fish, cause invertebrate drift into downstream habitats, decrease effectiveness in catching smaller fish and change fish behaviour (Elliot & Bagenal, 1972; Hudy, 1985; Frezza et al., 2003; Shoup et al., 2003; Fische et al., 2010). These limitations should be considered when designing and performing aquatic research.

Visual surveys are another research method used to study fishes and can be used to study fish population abundance, community composition, habitat use, competition and behaviour (Hankin & Reeves, 1988; Joyce & Hubert, 1998; Jordan et al., 2008; Ellender et al., 2012). In the past, underwater visual surveys were performed by snorkelers and SCUBA divers (Hankin & Reeves, 1988; Heggenes et al., 1990; Joyce & Hubert, 2003; Jordan et al., 2008). With technology becoming more advanced, accessible and affordable, the use of baited and unbaited underwater cameras as well as remotely operated vehicles has become increasingly used to study fishes (Frezza et al., 2003; Ellender et al., 2012; Ebner & Morgan, 2013; Santana-Garcon et al., 2014; Harasti et al., 2015; Misa et al., 2016). Compared to many traditional fisheries methods, visual surveys are less invasive and less likely to alter fish behaviour (Jordan et al., 2008; Ellender et al., 2012).

Lake Superior tributary streams provide habitat for multiple potamodromous fish species. Lake Superior potamodromous fish species migrate between lakes and their tributary streams at varying times during a year (Holm et al., 2009; Robillard et al., 2011). Potamodromous fish species like Brook Trout spawn in streams during the late summer and fall (Holm et al., 2009). Once juvenile Brook Trout emerge from their eggs, they will inhabit and grow in their natal tributary stream. Tributary streams provide a rich foraging habitat for juveniles due to the presence of high energy food sources and lack of predators (Miller & Sadro, 2003). Brook Trout in the Lake

Superior watershed exhibit two forms of migratory behaviour with a portion of the population staying in their natal streams (resident ecotype) and the other portion of the population spending some time in their natal streams before eventually migrating into Lake Superior (lake ecotype). For potamodromous fish species such as the Brook Trout, streams serve not only as a critical habitat for growing juveniles but also adult residents.

Fish can be sensitive to ecological disturbances such as changes in water temperature and dissolved oxygen (Richter & Kolmes, 2005). Habitat disturbance, fragmentation, loss, climate change and invasive species all have the potential to threaten fish populations (Marschall & Crowder, 1996; Huckins et al., 2008). Salmonids are particularly sensitive to environmental changes and adequate water and habitat quality is essential to their survival. Salmonids are a coldwater fish and temperature regulates many of their physiological processes (Baird & Krueger, 2003; Richter & Kolmes, 2005; High et al., 2006; Butryn et al., 2013). Prolonged exposure to warm water temperatures can be lethal for salmonids (Baird & Krueger, 2003; Lund et al., 2003; Richter & Kolmes, 2005; Butryn et al., 2013). Particularly in the summer months, stream water temperatures may approach and surpass lethal temperature levels for an individual fish. During these stressful conditions, cold-water fish must either avoid or acclimate to warm water environments.

Multiple species of salmonid have been observed behaviourally thermoregulating by migrating and occupying localized regions of cold water within a watershed (Baird & Krueger, 2003; Ebersole et al., 2003; Goniea et al., 2006; High et al., 2006; Tiffan et al., 2009; Petty et al., 2012). Localized regions of cold water are often referred to as thermal refuges and serve as a critical habitat for many fish species. Past studies have shown salmonid distribution within stream network is influenced by the presence of localized regions of thermal refugia (Torgerson et al., 1999; Baird & Krueger, 2003; Ebersole et al., 2003; Petty et al., 2012).

Multiple abiotic factors influence water temperatures observed in streams and these factors include climate, stream flow, geology, morphology, land use and the condition of the canopy and riparian vegetation surrounding the stream (Poole & Berman, 2001; Chu et al., 2008). Particularly in northern climates, surface runoff and groundwater temperatures are often colder than stream water temperatures. In these climates, accumulations of surface and shallow subsurface flow often add cooler water to localized regions of a stream (Poole & Berman, 2001). These regions of accumulated surface and shallow subsurface flow can maintain consistently cool and stable thermal conditions within a watershed and serve as thermal refugia for fish particularly during warm summer months (Poole & Berman, 2001; Baird & Krueger, 2003; Chu et al., 2008).

1.2 Study Area

Lake Superior is farthest north and west of all the Great Lakes, and is located between Ontario to the north, Minnesota to the west and Wisconsin and Michigan to the south. Not only is Lake Superior the largest in both surface area and volume among all the Great Lakes, but it also has the largest surface area of any freshwater lake in the world (Matheson & Munawar, 1978). Lake Superior has a volume of $\sim 12,000\text{km}^3$ and the Lake Superior drainage basin has a total surface area of $\sim 210,000\text{km}^2$, of which, 39% of the total surface area of the Lake Superior drainage basin is covered by the lake (Matheson & Munawar, 1978). The land surrounding the Lake Superior watershed is predominantly covered by forest (Matheson & Munawar, 1978). The watershed is situated almost entirely within the Canadian Shield which predominantly consists of igneous and metamorphic rocks that are strongly resistant to weathering and erosion (Matheson & Munawar, 1978).

Nipigon Bay, the northernmost portion of Lake Superior, is enclosed by the Black Bay Peninsula on the west and multiple small islands kilometers southeast of the town of Rosport, Ontario. Nipigon Bay is located within the boreal zone of Canada (Brandt et al., 2013). The climate that is typical of Nipigon Bay includes long winters with consistent below-freezing temperatures and periodic snowfall and warm summers that only span a few months (Warewick & Rubec, 1989). Due to this cold and harsh climate, forests in the area consist primarily of coldtolerant tree species such as firs, larches, spruces, pines, poplars and birches (Warewick & Rubec, 1989; Brandt et al., 2013). The region is defined by a moderate amount of topographic relief made up of granitic bedrock outcrops and glacially eroded valleys (Wickware & Rubec, 1989).

Shallow sandy soils containing loamy moraine are the predominant soil type of the region (Wickware and Rubec, 1989).

Microhabitat and reach spatial scale research was conducted on 10 tributary streams that flowed into the Nipigon Bay. Nipigon Bay and its tributary streams have, for the most part, experienced minimal development apart from some forest management activity and development of private property. Generally, streams in the Nipigon Bay watershed are high gradient and lacking in deep pools. Many of the Nipigon Bay tributary streams contain impassable barriers (often waterfalls) within 5 km upstream of Lake Superior (Mucha & Mackereth, 2008; Robillard et al., 2011). Salmonids within Nipigon Bay tributary streams include Brook Trout, Rainbow Trout, Lake Trout, Brown Trout, Chinook Salmon, Coho Salmon and Pink Salmon (*Salvelinus fontinalis*; *Oncorhynchus mykiss*; *Salvelinus namaycush*; *Salmo trutta*; *Oncorhynchus tshawytscha*; *Oncorhynchus kisutch*; *Oncorhynchus gorboscha*) (Holm et al., 2009).

1.3 General Methods

1.3.1 Site Selection

By analyzing digital elevation models using Esri ArcGIS (Version 10.1), predicted flow pathways were mapped for multiple streams within the Nipigon Bay watershed. Predicted flow pathways predict pathways of low elevation along a stream where surface runoff and shallow subsurface flow can accumulate and often contribute cooler water to a localized region of a stream. Of the multiple streams were visited in preliminary surveys, 10 contained suitable hydrological and thermal characteristics such as a manageable size to conduct stream surveys and the presence of potential thermal refugia created by a predicted flow pathway (Figure 1.1). Two 50 m sections (reaches) that could be reached on foot were selected in each of the 10 streams (Figure 1.2). Of these two reaches, one reach contained a predicted flow pathway (“inflow” reach) and the other reach did not contain a predicted flow pathway (“non-inflow” reach). Preliminary surveys ensured each inflow reach contained a localized region of thermal refugia. Stream temperatures were measured using a Thermo Plus water resistant thermometer (ThermoWorks, American Fork, Utah) and thermal refugia microhabitats were identified as microhabitats where the temperature at the stream-substrate interface was at least 1°C colder than the average substrate temperatures observed within the rest of the reach. All studied reaches were downstream of migratory barriers and at least 100m away from highways and major roads. Reaches were a minimum of 100m apart to reduce the likelihood the same salmonids would be observed in both reaches during given a survey event. The distance upstream (in kilometers) each studied reach was from the mouth to Lake Superior was calculated using the trace feature in Esri ArcGIS (Version 10.1). Site selection and preliminary surveys were conducted June 13 – July 5, 2018.

1.3.2 Stream Surveys

Standardized stream surveys were conducted to evaluate the physical and thermal characteristics at a microhabitat spatial scale within each reach. At 5 m intervals, habitat measurements were taken at each of 5 equidistant points across the width of the stream for every 5 m interval. Measurements included depth, substrate type, stream-substrate interface temperature and surface water temperature. The location, date, time, crew, weather condition, air temperature and reach dominant substrate (dominant substrate observed within the entire reach) were also recorded for each reach.

For each reach, a “cold” microhabitat was marked as the microhabitat with the coldest stream-substrate interface temperature observed within the entire reach. A “warm” microhabitat was marked as a microhabitat with relatively similar microhabitat characteristics as the cold

microhabitat (similar depth and substrate type) but with warmer stream-substrate interface temperatures. HOBO Pendant temperature data loggers (ONSET, Bourne, Massachusetts) attached to a brick were placed at the stream-substrate interface in locations marked as cold microhabitats to obtain hourly temperature data during the summer months. Temperature data loggers were also placed close to the surface of the water column within each non-inflow reach to obtain hourly stream surface water temperature data during the summer months. All stream surveys were conducted July 10 – August 9, 2018 between 11:00 and 18:00.

1.3.3 Video Surveys

Video surveys were conducted immediately after stream surveys for both cold and warm microhabitats within each reach (Figure 1.3). GoPro Hero 5 cameras (GoPro, San Mateo, California) attached to Manfrotto Compact Light tripods (Manfrotto, Markham, Ontario) were placed in locations near the centre of the stream with the lens focusing on a metal stake with orange flagging tape. This flag was placed 1 m in front of the camera lens and the area of stream captured in the camera's field of view up to the flag was considered the sampling area. This area was selected to ensure accurate detectability of fish and to standardize the area sampled at each microhabitat location. By measuring the horizontal distance captured by the camera at 1 m (1.88 m) and multiplying this distance by half of 1 m (area of a triangle = $1/2bh$), the sampling area was determined to be 0.94 m². Cameras were placed in locations as free of rocks, woody debris and aquatic vegetation as possible. Cold and warm cameras started recording footage at the same time and recorded for a minimum of one hour. All underwater video surveys were conducted July 10 – August 9, 2018 between 11:00 and 18:00.

1.3.4 Electrofishing Surveys

Three-pass electrofishing surveys were performed for both reaches in 8 of the 10 streams. These streams included Ruby Creek, Firehill Creek, Roxy Creek, East Ozone Creek, Dublin Creek, MacInnes Creek, Cypress River and Little Cypress River. Electrofishing surveys were not performed on Little Gravel River and Wesley Creek as these sites were deemed too difficult to access on foot. The downstream and upstream end of each reach were blocked with seine nets to prevent fish from entering or leaving the reach during shocking. Site name, date, water conductivity and start time were recorded. Using an Apex Backpack Electrofisher (SMITH-ROOT, Vancouver, Washington), horizontal sweeps across the width of the stream were performed moving upstream until the entire reach had been swept. Stunned fish were caught using nets and placed in a submerged bucket that had tiny holes in the bottom to provide water circulation and

oxygen located a sufficiently far distance downstream. At the end of each pass, fish were identified to species, weighed to the nearest gram, the total and fork lengths were measured (mm) and the shocking seconds were recorded. Electrofishing methods were repeated for a total of three passes. After the final pass, the end time and shocking seconds was recorded. The nets were removed from the stream and all fish caught were released back into the stream. Total salmonid catch was divided by the total shocking seconds to generate salmonid catch-per-minute for each reach. All electrofishing surveys were conducted August 13 – August 19, 2018 between 10:00 and 17:00.

1.3.5 Video Analysis

Thirty individual minutes of video were randomly selected from a minimum of an hour of video for each microhabitat. Within each subsampled minute of video, every salmonid observed swimming within the sampling area was recorded and the time, in seconds, when the individual entered and left the frame was recorded. Fish observed outside the sampling field were not recorded. Salmonid MaxN (measured by counting the maximum number of salmonids present in the camera's field of view at the same time for a given subsampled minute) as well as salmonid presence/absence was recorded for every subsampled minute. Due to extremely high salmonid densities observed in the East Ozone Creek microhabitats, MaxN in East Ozone Creek microhabitats could not be accurately determined using standardized video analysis methods and was not performed for East Ozone Creek microhabitats. At one site the video files were corrupted and thus salmonid data are missing from one microhabitat in Firehill Creek (39 observations instead of 40).

1.4 Tables and Figures

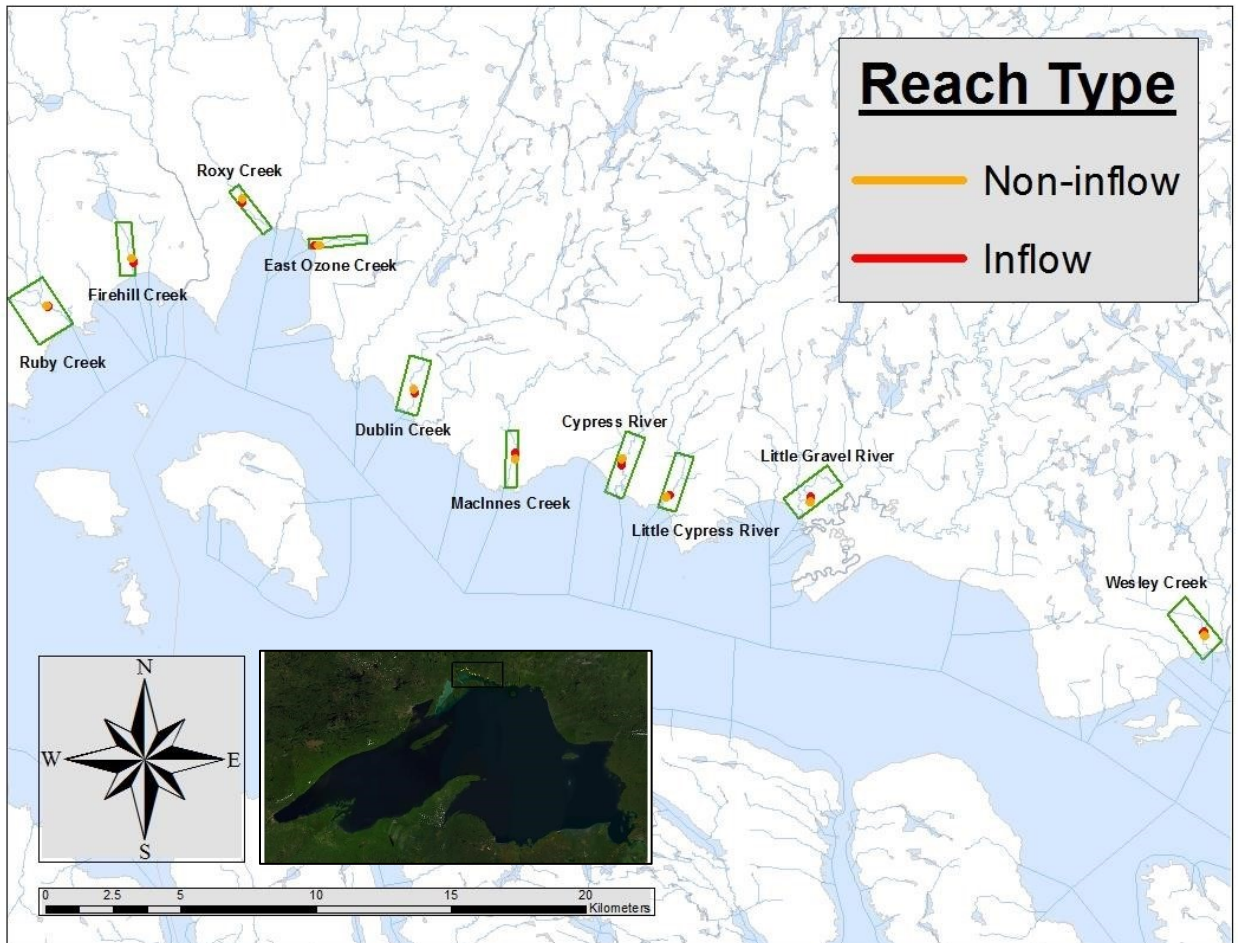


Figure 1.1. Map of the Nipigon Bay and the 10 studied tributary streams. The 10 studied streams include Ruby Creek, Firehill Creek, Roxy Creek, East Ozone Creek, Dublin Creek, MacInnes Creek, Cypress River, Little Cypress River, Little Gravel River and Wesley Creek.

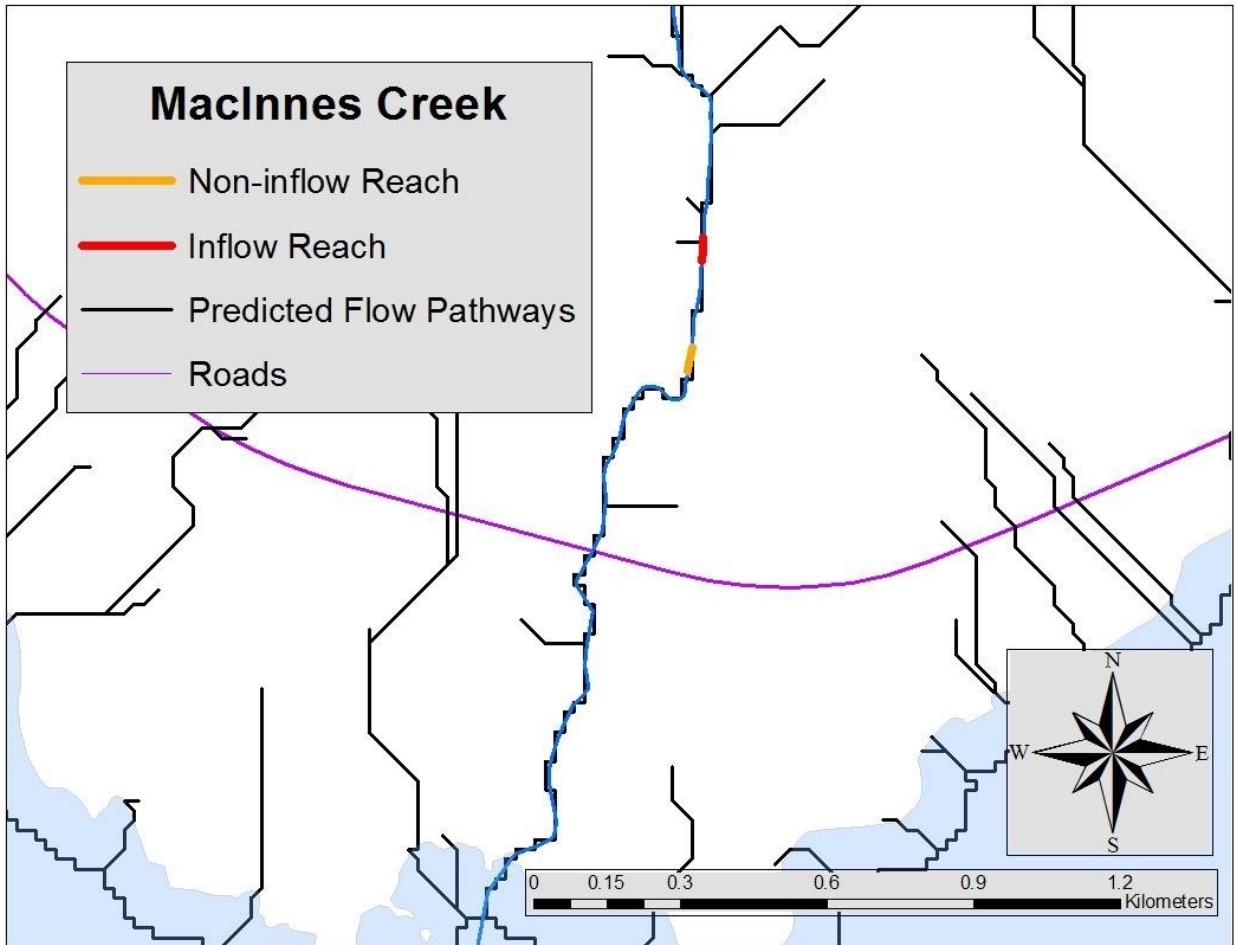


Figure 1.2. Example of the GIS project and layers used to locate stream reaches that contain localized regions of thermal refugia. Figure shows the approximate locations of all predicted flow pathways along the MacInnes Creek.

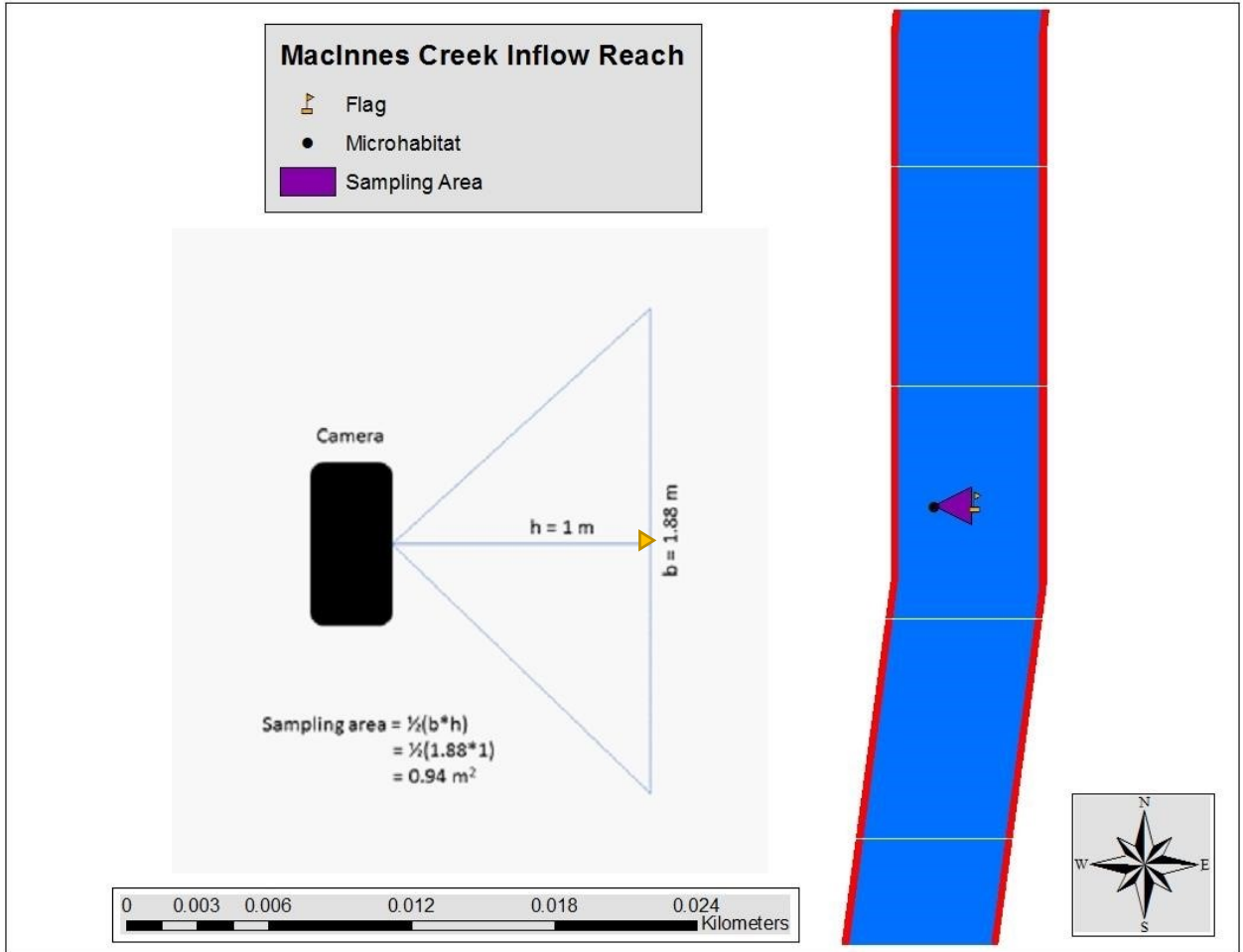


Figure 1.3. Example of microhabitat surveys and underwater camera placement at the cold microhabitat within the MacInnes Creek inflow reach. Figure also shows how the visual sampling area was calculated (sampling area = 0.94 m²).

Chapter 2. Evaluation of unbaited underwater cameras as an alternative method to study stream-dwelling salmonids

2.1 Abstract

Traditional research methods used in streams such as angling, electrofishing, netting and the use of various piscicides have the potential to harm sampled fish. In recent years, some researchers have used baited underwater cameras as a less invasive alternative to study stream-dwelling fishes. As the main goal of the study was to compare salmonid relative abundance estimates obtained from underwater visual surveys and electrofishing, unbaited camera methods were developed to observe salmonid habitat use at a microhabitat spatial scale (~1 m²). Stream research was conducted in 10 tributary streams within the Nipigon Bay watershed in Ontario, Canada. At each stream, visual surveys using unbaited underwater cameras were performed at two microhabitats within two reaches (50 m). Three-pass electrofishing surveys were also performed at each reach. Precision analyses were used to determine a standardized minimum number of randomly subsampled minutes of video needed to generate precise salmonid relative abundance estimates for all stream microhabitats. Salmonid relative abundance (mMaxN) and probability of occupancy were calculated using 23 randomly subsampled minutes of video. Salmonid catch-per-minute was calculated for all electrofishing surveys. A significant positive relationship was observed between electrofishing catch-per-minute and video-based mMaxN as well as between electrofishing catch-per-minute and video-based probability of occupancy ($p < 0.05$). One limitation of the unbaited visual surveys methods used in this study was the extreme difficulty in accurately identifying juvenile salmonid species observed in the video as factors such as observing small fish, observing fish close to the 1 m boundaries, observing fish in habitats with poor visibility and observing fish which spend milliseconds in the camera's field of view all impeded the accurate species identification of salmonid fry and parr. Despite these challenges, results of this study indicate that visual surveys are less invasive but similarly accurate as other research methods used to study fishes at different spatial scales.

2.2 Introduction

Traditional research methods used in fisheries science such as angling, electrofishing, netting and the use of various piscicides all have the potential to harm sampled fish (Elliot & Bagenal, 1972; Hudy, 1985; Frezza et al., 2003; Bartholomew & Bohnsack, 2005; Clearwater et al., 2008). Electrofishing generates an electric current underwater which can immobilize nearby fish making them easier to catch and is commonly used for sampling fish in stream and rivers. Electrofishing is an effective method for sampling individual fish and incorporation of multiple surveys (or passes) allows researchers to determine fish population and community abundance within a given sampling area (Zippin, 1956; Frezza et al., 2003).

Though generally considered to be a reliable method for studying fishes, electrofishing methods have limitations that should be considered when studying fishes and fish communities. Electrofishing can cause immediate and delayed harm to shocked fish including burns, visible abnormalities, fractured/dislocated vertebrae and immediate or delayed mortality (Hudy, 1985). Mortality in shocked fish is suspected to be caused by respiration failure, hemorrhaging, fractured vertebrae or a combination of the above effects (Hudy, 1985). Electrofishing activities can also cause invertebrates to become dislodged from the substrate they are occupying and subsequently drift downstream (Elliot & Bagenal, 1972).

Efficiency of electrofishing increases exponentially with fish length as the voltage gradient (or difference in voltage from head to tail) is greater in longer fish and thus they are more likely to become immobilized by the electrofishing unit (Bohlin et al., 1989). As well as being easier to immobilize, larger fish are also easier to see in the water column and thus more easily captured. Both factors contribute to a potential bias towards catching larger fish during electrofishing activities. A similar catch bias can be observed when netting, as the net dimensions and mesh size determine the minimum size of fish that can be caught (Shoup et al., 2003; Fische et al., 2010). A large fish bias can influence fisheries estimates such as relative abundance, size structure, and species composition as the decreased effectiveness in catching smaller fish can yield abundance estimates in a sampled unit that are lower than the true abundance of that unit (Frezza et al., 2003; Shoup et al., 2003; Fische et al., 2010).

Electrofishing may also cause changes in fish behaviour as well as their subsequent response to incoming electric currents. Depending on where fish are located relative to the electric field, they may flee from, or be attracted to the produced electric current (Heggenes et al., 1990; Ensign et al., 2002; Frezza et al., 2003). This alteration in fish behaviour and response can be a major limitation when using electrofishing to study fish ecology especially when studying fish habitat use. As fish response to electric currents can alter the distribution of fish within an

ecosystem, conclusions about fish habitat use at smaller spatial scales would be unreliable (Heggenes et al., 1990; Ensign et al., 2002; Frezza et al., 2003).

Because electrofishing may bias sampling efforts and have harmful effects on both individual fish and fish communities, many researchers have adopted less invasive methods to study fishes, especially when conducting research in areas where threatened fish species are present. Visual surveys can be used to study multiple aspects of aquatic ecology such as fish population abundance, community composition, habitat use, competition and behaviour (Hankin & Reeves, 1988; Joyce & Hubert, 1998; Jordan et al., 2008; Ellender et al., 2012). Besides being less invasive, visual surveys are also considered to be less likely to alter fish behaviour (Jordan et al., 2008; Ellender et al., 2012). Until recently, most underwater visual surveys were performed by snorkelers and SCUBA divers (Hankin & Reeves, 1988; Heggenes et al., 1990; Joyce & Hubert, 2003; Jordan et al., 2008). With technology becoming more advanced, accessible and affordable, the use of baited and unbaited underwater cameras as well as remotely operated vehicles has become increasingly used in fisheries science (Frezza et al., 2003; Ellender et al., 2012; Ebner & Morgan, 2013; Santana-Garcon et al., 2014; Harasti et al., 2015; Misa et al., 2016). Once underwater footage is obtained, subsequent video analysis methods can be used to obtain a relative abundance estimate of fish observed within the camera's field of view (Ellender et al., 2012; Ebner & Morgan, 2013; Santana-Garcon et al., 2014; Harasti et al., 2015; Misa et al., 2016). The maximum number of fishes in the frame at one instance during a given interval of time (MaxN) is a relative abundance estimate that is often used in visual surveys (Ellender et al., 2012; Ebner & Morgan, 2013; Santana-Garcon et al., 2014; Harasti et al., 2015; Misa et al., 2016).

Several studies have evaluated the use of visual surveys to study stream dwelling fish populations and obtain abundance estimates (Heggenes et al., 1990; Joyce & Hubert, 2003; Ellender et al., 2012). Visual survey methods can include surface observations, diver observations and observations by both baited and unbaited underwater cameras. The reported strength of relationships between visual survey measurements and electrofishing measurements varied among studies (Heggenes et al., 1990; Joyce & Hubert, 2003; Ellender et al., 2012). Heggenes et al. (1990) compared the number of Brown Trout (*Salmo trutta*) and Atlantic Salmon (*Salmo salar*) observed using surface observation, diver observation and electrofishing methods noting that the three methods yielded widely different estimates of salmonid abundance. However, Joyce & Hubert (2003) found a significant linear relationship between electrofishing depletion estimates and diver fish counts for both Cutthroat Trout (*Oncorhynchus clarkii*) and Brown Trout (*Salmo trutta*). Finally, Ellender et al. (2012) compared the relative abundance Eastern Cape Redfin

(*Pseudobarbus afer*) and Cape Kurper (*Sandelia capensis*) obtained using unbaited underwater cameras and electrofishing methods and found a significant correlation between visual estimates of MaxN and electrofishing catch-per-unit-effort.

Like other methods used to study fishes, the effectiveness of visual surveys and underwater video analysis can be limited by environmental and biological factors. Certain aquatic habitats are not favourable to conduct visual surveys (e.g. turbulent flows) and objects that obstruct the camera's field of view can lead to poor quality video footage (Frezza et al., 2003). Underwater video footage with poor visibility impedes an observer's ability to identify and study the fish occupying the habitat observed within the camera's field of view (Frezza et al., 2003).

Occupancy modelling has a wide range of scientific and management applications to study and monitor populations (single species models) or communities (multi-species models) when sampling methods have some proportion of detection error (MacKenzie et al., 2002; Welsh et al., 2013; Bailey et al., 2014). Occupancy modelling has been used to study species distribution and habitat use, as well as study aspects of community ecology such as invasive species interactions, competition and predation (MacKenzie et al., 2002; Welsh et al., 2013; Bailey et al., 2014). A staple of occupancy modelling is the standard use of presence/absence data (MacKenzie et al., 2002; Welsh et al., 2013; Bailey et al., 2014). Presence/absence data generally requires less effort to collect and analyze compared to traditional methods of abundance estimation (Joseph et al., 2006; Hui et al., 2009). Occupancy models use presence/absence data, along with various site and sampling covariates, to generate probabilities of detection and occupancy and analyze covariate relationships among and within study sites (MacKenzie et al., 2002; Welsh et al., 2013; Bailey et al., 2014). Poor water conditions and habitat characteristics can often make detection of fish difficult. Therefore, use of occupancy models that account for poor survey conditions and imperfect detection could yield highly accurate probabilities of occupancy within a given study area.

My goal was to compare salmonid relative abundance estimates obtained from underwater visual surveys and electrofishing. The first objective was to determine a standardized minimum effort (number of randomly subsampled minutes of video) needed to generate precise salmonid relative abundance estimates for all stream microhabitats. The second objective was to evaluate relationships between reach (50 m section of stream) electrofishing catch-per-unit-effort and estimates of abundance and occupancy derived from visual surveys observed at two microhabitats (~1 m²) within the reach.

2.3 Methods

For field data collection methods, refer to the General Methods section (1.3).

2.3.1 Data Analysis

In the context of this study, precision analyses refer to the methods that examine the accuracy of salmonid relative abundance estimates compared to the true abundance of salmonids within a given spatial scale. Precision analyses were performed to determine the minimum number subsampled minutes needed to obtain precise estimates of salmonid mean MaxN (mMaxN) for all sampled microhabitats. The absolute difference microhabitat mMaxN estimates changed with the addition of each subsampled minute was calculated and the mean absolute percent difference mMaxN changed among all microhabitats with the addition of each subsampled minute was plotted. The absolute percent difference (difference in mMaxN divided by mMaxN) microhabitat mMaxN estimates changed with the addition of each subsampled minute was calculated and mean absolute percent difference among all microhabitats with the addition of each subsampled minute was determined. Finally, the standard error of absolute percent differences with the addition of each subsampled minute was determined. Mean absolute percent difference and standard error of absolute percent differences were plotted and tested using the linear model function in R (Version 3.5.3). Residual plots were made for all tested relationships to ensure they met the assumptions of linear regression. The slopes and y-intercepts of the mean absolute percent difference and standard error of absolute percent differences regression lines were recorded and used to create positive and negative error lines. To calculate the slope (m) and y-intercept (b) of the positive error line:

$$m = (m \text{ of the mean absolute percent difference regression line}) + (m \text{ of the standard error of absolute percent differences regression line})$$

$$b = (b \text{ of the mean absolute percent difference regression line}) + (b \text{ of the standard error of absolute percent differences regression line})$$

$$\text{Positive error line } \rightarrow y = -0.3743x + 13.59418$$

To calculate the slope (m) and y-intercept (b) of the negative positive error line:

$$m = (m \text{ of the mean absolute percent difference regression line}) - (m \text{ of the standard error of absolute percent differences regression line})$$

$$b = (b \text{ of the mean absolute percent difference regression line}) - (b \text{ of the standard error of absolute percent differences regression line})$$

$$\text{Negative error line } \rightarrow y = -0.18338x + 6.66646$$

Once positive and negative error lines were created, the minute (x) where positive error line decreased to 5% mean absolute percent difference ($y = 5$) was calculated. This determined the minimum number of randomly subsampled minutes required to obtain 95% precision in relative abundance estimates for all sampled microhabitats accounting for error.

Once the minimum number of randomly subsampled minutes was determined, salmonid reach mMaxN as well as probability of occupancy was calculated for each microhabitat. Salmonid reach mMaxN was calculated as the mMaxN between the cold and warm microhabitats. To calculate salmonid microhabitat probability of occupancy, salmonid presence/absence data was placed chronologically into a spreadsheet with each randomly subsampled minute of video treated as an independent sampling event (or detection history). The detection covariates used for occupancy modelling were the presence/absence of cloud cover, microhabitat depth and substrate type. Detection covariates chosen were either supported by past scientific literature or were based on observations made during the study. Due to a limited number of studied microhabitats, only 5 occupancy covariates were used. These covariates included stream sampled, reach type (inflow or non-inflow) and microhabitat type (cold or warm), date sampled (Julian day relative to day 192) and the time sampled (hour relative to 16:00). All occupancy modelling was performed using the occupancy modelling software PRESENCE (Version 2.12.22). First, the top detection model was obtained by modelling every combination of detection covariate. Using the top detection model, every combination of occupancy covariate was modelled. The Results Browser in PRESENCE was used to create an AIC table. The output of the top occupancy model yielded the probability of occupancy of each microhabitat.

The relationships between reach electrofishing catch-per-minute and reach mMaxN as well as probability of occupancy were tested using the linear model function in R. All relationships were also plotted using R and residual plots were examined to ensure tested relationships met the assumptions of linear regression. The relationship between catch-per-minute and reach mMaxN was found to be non-linear and reach mMaxN values received a log base 10 transformation. The relationship between catch-per-minute and probability of occupancy was also found to be non-linear and catch-per-minute values received a log base 10 transformation.

2.4 Results

2.4.1 Precision Results

Mean absolute difference in mMaxN among all microhabitats decreased with the addition of each subsampled minute (Figure 2.1). After roughly 10 randomly subsampled minutes, absolute differences in calculated mMaxN values with the addition of each subsampled minute became increasingly minimal.

The mean absolute percent difference in mMaxN among all microhabitats decreased with the addition of each subsampled minute (Figure 2.2). This decrease was both linear and significant ($F_{[1,27]} = 42.72$; $p < 0.05$; $r^2 = 0.60$). Standard error of absolute percent differences among all microhabitats decreased with the addition of each subsampled minute (Figure 2.2). This decrease was both linear and significant ($F_{[1,27]} = 18.94$; $p < 0.05$; $r^2 = 0.39$). Accounting for error, the minimum number of randomly subsampled minutes needed to obtain 95% precision in relative abundance estimates for all microhabitats was calculated to be 22.96 minutes (rounded to 23).

2.4.2 Occupancy Modelling Results

Occupancy models used data obtained through underwater camera surveys and stream surveys to determine probability of occupancy for each microhabitat (Table 2.1). The best detection model contained the detection covariates cloud cover, depth and substrate type (detection model was 7.35 AIC units higher than the best occupancy model). *Cloud cover*, *depth* and *substrate type* were included as probability of occupancy covariates used when running occupancy models. The top occupancy model included stream sampled as an occupancy covariate and cloud cover, depth and substrate type as detection covariates.

2.4.3 Video - Electrofishing Results

Salmonid MaxN and presence/absence from 23 randomly subsampled minutes and electrofishing survey data was used to calculate salmonid catch-per-minute, cold mMaxN, warm mMaxN, reach mMaxN and probability of occupancy for all microhabitats (Table 2.2).

The relationship between catch-per-minute and reach mMaxN was found to be nonlinear, so mMaxN values were log base 10 transformed. There was a significant positive linear relationship between catch-per-minute and reach $\log(\text{mMaxN} + 1)$ ($F_{[1,12]} = 21.67$; $p < 0.05$; Figure 2.3). The catch-per-minute and reach $\log(\text{mMaxN} + 1)$ linear model performed fairly well in explaining the variability between catch-per-minute and mMaxN relative abundance estimates ($R^2 = 0.61$).

The relationship between catch-per-minute and probability of occupancy was found to be nonlinear, so catch-per-minute values were log base 10 transformed. There was a significant positive linear relationship between $\log(\text{catch-per-minute})$ and probability of occupancy ($F_{[1,12]} = 50.11$; $p < 0.05$;

Figure 2.4). The log(catch-per-minute) and probability of occupancy linear model performed well in explaining the variability between catch-per-minute and probability of occupancy relative abundance estimates ($R^2 = 0.79$).

2.5 Discussion

Significant positive relationships were observed between microhabitat scale estimates of abundance and occupancy derived from visual surveys and reach scale catch-per-minute derived from electrofishing surveys. A significant positive relationship between microhabitat probability of occupancy and reach catch-per-minute is consistent with past studies that have shown positive relationships between species occupancy and abundance (He & Gaston, 2000; Holt et al., 2002). As recording the presence-absence of a taxonomic group, such as the family *Salmonidae*, instead of a single target species has seemingly never been performed before (multi-species occupancy models are used if one wishes to study occupancy of multiple species), this significant positive relationship between microhabitat probability of occupancy and reach catch-per-minute is somewhat unexpected. A challenge associated with occupancy modelling regards studying target species that are very common as occupancy-covariate relationships can be difficult to determine if a target species is present in almost all detection histories. Random subsampling of individual minutes of video to create multiple detection histories provides a potential solution for studying common fish species. Salmonid microhabitat movements often varied among randomly subsampled minutes within a given microhabitat resulting in a greater variation of microhabitat presence/absence.

The best detection model contained all assumed influential detection covariates (cloud cover, depth and substrate type). In the best occupancy models, estimates of detection were higher when surveying on cloudy days. This is an unexpected result because cloud cover was thought to darken the resulting video making an observer's ability to detect salmonids more difficult. However, cloud cover may reduce the glare observed in underwater footage, making salmonids easier to detect. As expected, probability of detection decreases at greater water depths likely due to a reduction in light at greater water depths. Light reduction was very pronounced the few microhabitats that were deep pools and reduced the ability to detect salmonids. Microhabitats with larger substrates such as boulders (and cobbles to a lesser extent) had a higher probability of detection compared to points with finer substrate types such as silt and gravel. This was likely due to poor water clarity in silt sites which reduces visibility and detectability in the videos.

Occupancy covariates also explained the heterogeneity observed within the presence/absence data with the most influential covariate being the stream that was sampled. Stream being a highly influential occupancy covariate was likely due to unique landscape habitat characteristics and ecological processes occurring in an individual stream not captured with the covariates used in this study, resulting in variable salmonid abundances and probability of occupancies among studied Nipigon Bay tributary streams (Stanfield et al., 2006; Deschenes &

Rodriguez, 2007). Though use of stream as an occupancy covariate may account for the unique characteristics of individual streams, it itself is not a measurable habitat characteristic. The time, date and reach type (probability of occupancy was higher in reach that contained predicted flow pathways) also explained heterogeneity observed within the presence/absence data, but to a lesser extent. Microhabitat type (cold or warm) was the least influential occupancy covariate.

A significant positive relationship was observed between point mMaxN and reach catch-per-minute which is consistent with past studies (Ellender et al., 2012). However, only 61% of the variability in microhabitat mMaxN was explained by reach catch-per-minute. Compared to microhabitat probability of occupancy estimates obtained from this study, mMaxN performed worse as a predictor of reach catch-per-minute or relative abundance. This result is unexpected as it was assumed the added effort used to quantify salmonid relative abundance in the form of mMaxN would produce better fitting linear models. The poor fit of the mMaxN model compared to the probability of occupancy model was likely due to the considerable variation in salmonid relative abundance occurring among microhabitats within a reach. The best occupancy model did not include reach or microhabitat type as occupancy covariates and thus only calculated probability of occupancy for a given stream. Therefore, stream probability of occupancy better explained variability in reach catch-per-minute compared to reach mMaxN.

The minimum effort or number of randomly subsampled minutes of video needed to obtain 95% relative abundance precision in all Nipigon Bay stream microhabitats was roughly 23 minutes. Results from this study provide a good example of some key underwater video analysis concepts. Soak time (also referred to as set time or deployment time) refers to the length of time a camera was placed underwater and recording video. In the context of this study, soak time also refers to the number of randomly subsampled minutes of video used in obtaining mMaxN as well as probability of occupancy estimates. Precision, within the context of this study, refers to how close these estimates are to each other with varying soak times. Past studies have used cumulative and relative abundance curves to illustrate relationships between mean cumulative MaxN (% of MaxN) and increasing soak times (Ellender et al., 2012; Santana-Garcon et al., 2014; Harasti et al., 2015; Misa et al., 2016). Though these past analyses have been effective in determining appropriate soak times, this study considers changes in the difference and percent difference of relative abundance estimates observed among all cameras with increasing soak time. As mMaxN is a measurement of relative abundance, expressing changes to MaxN estimates as a percentage seemingly works well in determining a standardized minimum effort needed for all sites.

The results of this study support past studies that have shown precision in relative abundance estimates increases with soak time (Ellender et al., 2012; Santana-Garcon et al., 2014; Harasti et al., 2015; Misa et al., 2016). The use of mean absolute percent difference and standard error of absolute percent differences allows one to determine adequate soak times or number of randomly subsampled minutes based on the percentage relative abundance estimates change over time. The tested relationship between mean difference, as well as mean percent difference, in relative abundance estimates and soak time also shows that excessive soak times (greater than 23 randomly subsampled minutes) provided minimal improvements in the precision of relative abundance estimates and are an inefficient use of one's effort. A minimum soak time of 23 minutes is consistent with past studies that have examined relationships between soak time and precision (Ellender et al., 2012; Santana-Garcon et al., 2014; Harasti et al., 2015; Misa et al., 2016). Ellender et al. (2012) stated that 95% precision in mMaxN estimates is reached using a soak time of 22 minutes for Eastern Cape Redfin (*Pseudobarbus afer*) and a soak time of 15 minutes for Cape Kurper (*Sandelia capensis*). Harasti et al. (2015) studied fish in rocky reefs on the east coast of Australia stating that a soak time of 30 min provides precise estimates of fish relative abundance. Misa et al. (2016) performed camera surveys in the Hawaiian Islands stating that a soak time of 15 minutes is the minimum soak time that can be used while also achieving precise estimates of fish relative abundance. Among studies that used underwater cameras to estimate fish relative abundance, only Santana-Garcon et al. (2014) did not support implementing soak times of 30 minutes or less stating that a soak time of 120 minutes is optimal when performing camera surveys in tropical or warm-temperate areas.

A limitation of the visual methods used in this study was the extreme difficulty in accurately identifying the salmonid species observed in the video. The original objective of this study was to research the thermal habitat use of stream-dwelling Brook Trout (*Salvelinus fontinalis*). However, accurately identifying the juvenile Brook Trout among other juvenile salmonids observed in the video was often not possible. Factors such as observing small fish, observing fish close to the 1m boundaries, observing fish in habitats with poor visibility and observing fish which spend milliseconds in the camera's field of view all impeded the accurate species identification of salmonid fry and parr. Use of baited camera methods may have improved salmonid identification. Baited underwater cameras may make salmonid identification easier by increasing the amount of time fish stay in a sampling area as well as attracting fish to occupy microhabitats that are directly in front of the camera lens for optimal viewing. However, baited camera methods would not be suitable for studying fish microhabitat use or behaviour as fish attraction to bait would alter the natural behaviour of observed fishes.

Multiple salmonid species spawn in Nipigon Bay tributary streams such as Brook Trout, Rainbow Trout, Brown Trout, Chinook Salmon, Coho Salmon and Pink Salmon (*Salvelinus fontinalis*; *Oncorhynchus mykiss*; *Salmo trutta*; *Oncorhynchus tshawytscha*; *Oncorhynchus kisutch*; *Oncorhynchus gorbuscha*) (Holm et al., 2009). Brook Trout, Brown Trout, Coho Salmon, Chinook Salmon and Pink Salmon all spawn during the late summer and fall (Holm et al., 2009). Unlike other salmonids in the region, Rainbow Trout primarily spawn in the spring (Holm et al., 2009). Due to these life history differences among Nipigon Bay salmonids, the least developed juvenile salmonids observed in the video footage were likely Rainbow Trout. However, water temperature influences the development of salmonid eggs, with egg development and emergence time occurring over a shorter period in warmer water temperatures (Beacham & Murray, 1990). As water temperatures are warmer in spring compared to winter, Rainbow Trout eggs would theoretically develop faster than eggs of all other salmonid species in the region and thus visible differences between juvenile Rainbow Trout and all other juvenile salmonids may be less distinguishable than expected. Even in the best conditions, visual species identification of salmonids in the fry and parr life stages can be difficult as salmonids lack the distinguishable colouration observed in adults and thus species identification is easiest when individual fish are captured.

My results demonstrate the utility of visual surveys to estimate salmonid relative abundance as they are significantly correlated with survey methods at larger spatial scales. The significant relationships between salmonid relative abundance estimates obtained through microhabitat scale visual surveys and reach scale electrofishing surveys support the use of visual surveys to estimate salmonid relative abundance at larger spatial scales. However, models which used MaxN were not as accurate as models that predicted salmonid probability of occupancy based on the stream that was sampled. Models estimating microhabitat relative abundance (mMaxN) may have performed poorly compared to occupancy models due to the substantial variation in salmonid distribution and abundance that can occur at microhabitat and reach spatial scales (Fausch, 1993; Ecret & Mihuc, 2013). Therefore, improved methods that account for the potentially high variation in salmonid abundance observed at different spatial scales are needed to precisely estimate fish relative abundance at larger spatial scales. For future projects, distance sampling concepts (e.g. point sampling concepts) could potentially be applied to microhabitat visual survey methods to estimate fish relative abundance at over larger areas such as a reach or even a stream. However, improved methods such as standardized camera placement within stream microhabitats and more camera replicates would likely be needed in order to obtain estimates that more accurately represent the true abundance of fish within a given area.

2.6 Tables and Figures

Table 2.1. AIC table showing ranking of detection and occupancy models for salmonid occupancy in Nipigon Bay stream microhabitats.

Detection covariates	Occupancy covariates	deltaAIC	AIC weight	Model likelihood
Cloud cover + depth + substrate type	Stream	0	0.2136	1
Cloud cover + depth + substrate type	Stream + time	0.37	0.1775	0.8311
Cloud cover + depth + substrate type	Stream + date	0.95	0.1328	0.6219
Cloud cover + depth + substrate type	Stream + reach	1.61	0.0955	0.4471
Cloud cover + depth + substrate type	(None)	7.35	0.0054	0.0253
(None)	(None)	172.48	0	0

Table 2.2. Calculated reach catch-per-minute, cold mMaxN, warm mMaxN, reach mMaxN and probability of occupancy obtained using data from three-pass electrofishing surveys and 23 randomly subsampled minutes of video.

Reach	CPM	mMaxN			Psi
		Cold	Warm	Reach	
Cypress_inflow	0.5358	0.0435	0.3478	0.1957	1
Cypress_noninflow	0.2825	1.0435	1	1.0218	1
Dublin_inflow	0.6221	1.1739	0.1739	0.6739	0.7672
Dublin_noninflow	0.4165	0.2609	0	0.1305	0.7672
EastOzone_inflow	1.1251	NA	NA	NA	NA
EastOzone_noninflow	2.2173	NA	NA	NA	NA
Firehill_inflow	0.0418	0	0.0435	0.0218	0.3333
Firehill_noninflow	0.1553	NA	0	0	0.3333
Lilcypress_inflow	0.2491	0.2609	0.6087	0.4348	0.75
Lilcypress_noninflow	0.176	0.5652	0	0.2826	0.75
Lilgravel_inflow	NA	1	0.0435	0.5218	1
Lilgravel_noninflow	NA	0.8261	0.1739	0.5	1
Macinnes_inflow	0.8696	0.2174	2.7826	1.5	1
Macinnes_noninflow	0.7314	1.3913	2.6087	2	1
Roxy_inflow	0.0178	0	0	0	0
Roxy_noninflow	0.0484	0	0	0	0
Ruby_inflow	0.2196	0	0.0435	0.0218	0.5
Ruby_noninflow	0.1949	0.0435	0	0.0218	0.5
Wesley_inflow	NA	0.3043	3.2174	1.7609	1
Wesley_noninflow	NA	0.3043	0.6087	0.4565	1

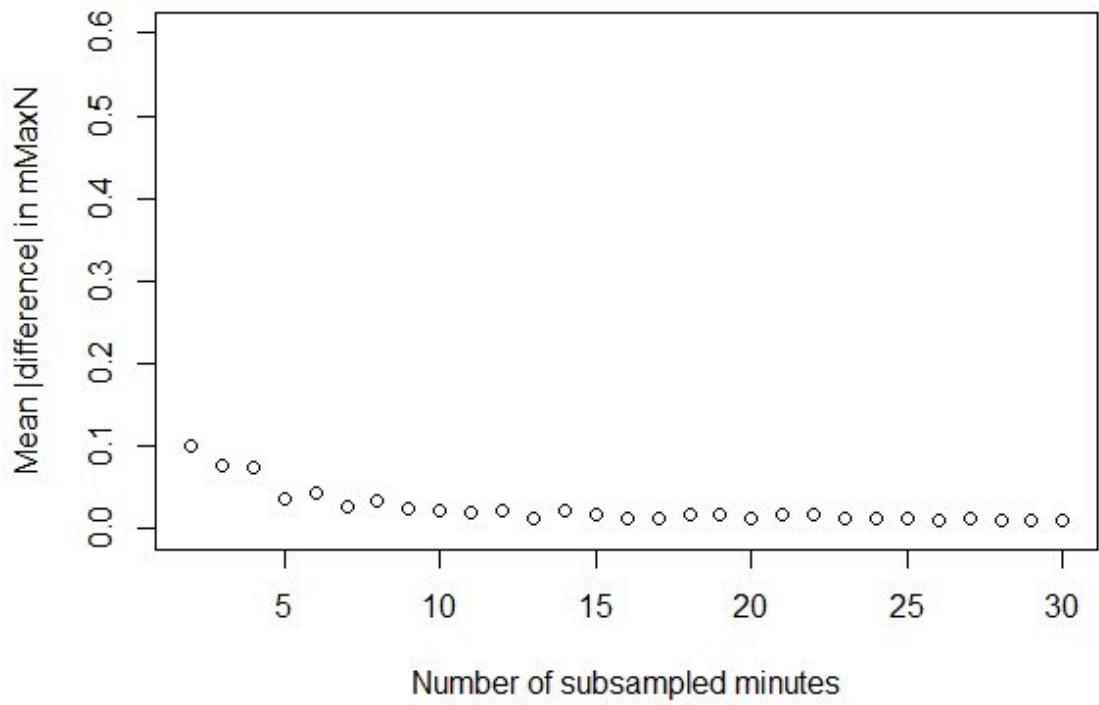


Figure 2.1. Mean absolute difference in mMaxN among all microhabitats with the addition of each subsampled minute.

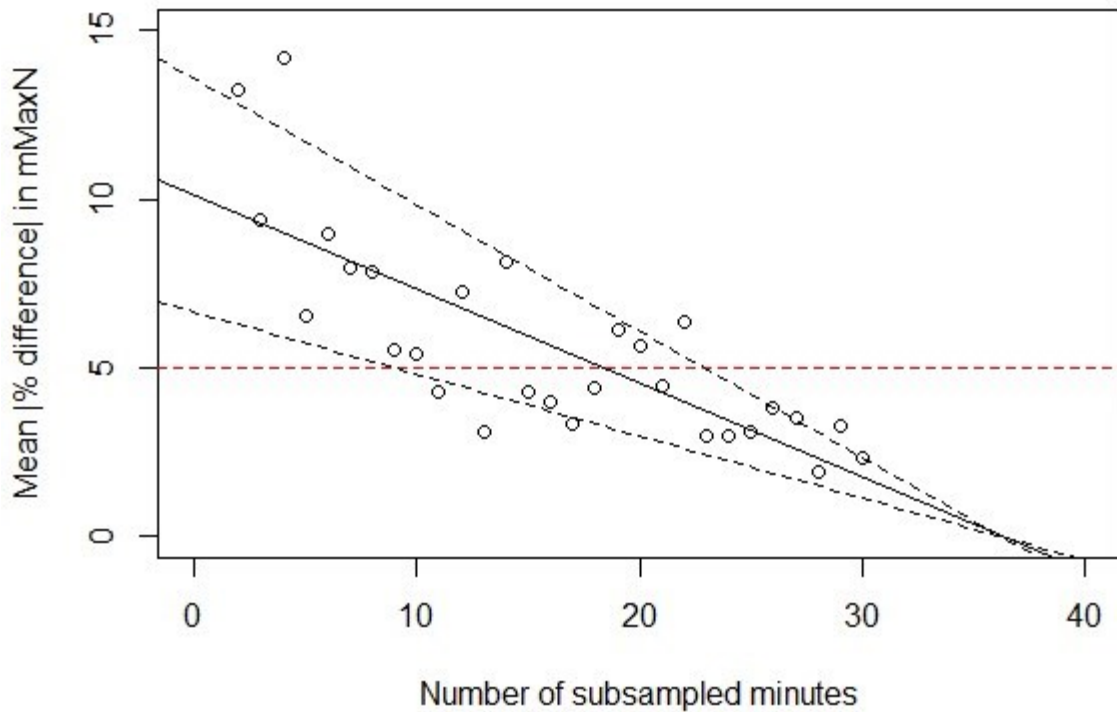


Figure 2.2. Mean absolute percent difference in mMaxN among all microhabitats with the addition of each subsampled minute. The black line denotes a calculated regression line. Black dashed lines denote the positive and negative error lines showing a decrease in the error of absolute percent differences with the addition of each subsampled minute. Red dashes line denotes an absolute percent difference in mMaxN of 5% (95% precision in calculated mMaxN estimates).

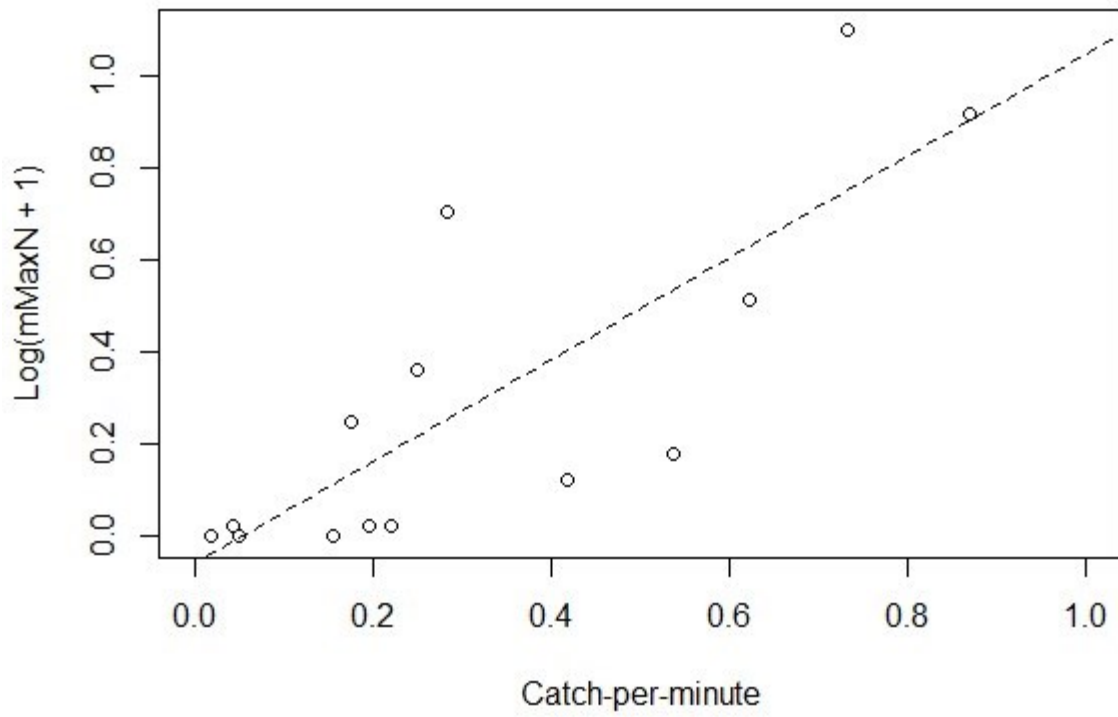


Figure 2.3. Plotted relationship between catch-per-minute and reach $\log(m\text{Max}N + 1)$. The black dashed line denotes a calculated regression line ($y = 1.10432x - 0.05906$).

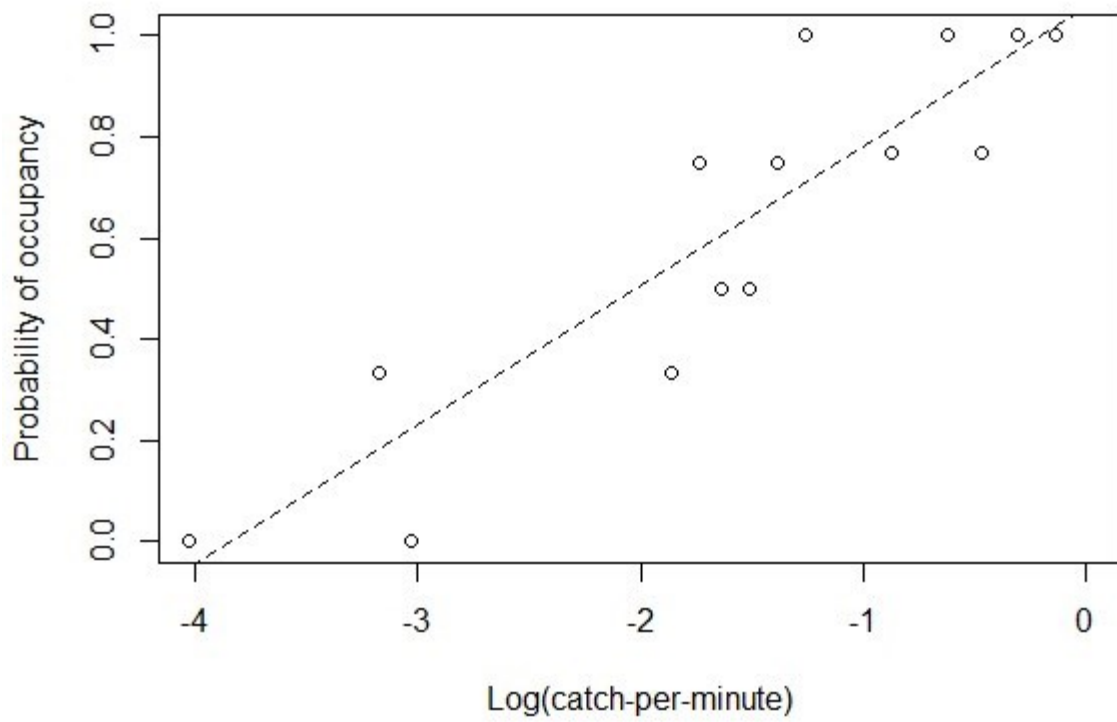


Figure 2.4. Plotted relationship between $\log(\text{catch-per-minute})$ and probability of occupancy. The black dashed line denotes a calculated regression line ($y = 0.27541x + 1.05554$).

Chapter 3. Influence of temperature on salmonid habitat use at multiple spatial scales in Lake Superior tributaries

3.1 Abstract

Several salmonid species have been observed occupying Lake Superior tributary streams at different times within a year. Many of these species exhibit complex migratory and spawning behaviours. For some potamodromous salmonid species like Brook Trout, streams serve not only as critical spawning habitat but also habitat for juveniles and stream residents year-round. As salmonids are cold-water fishes, cooler stream water temperatures are essential for individuals to avoid temperature stress and in extreme cases death. To avoid temperature stress, thermoregulatory behaviour and the use of thermal refuges have been observed in multiple salmonid species. Relationships between stream thermal habitat characteristics and salmonid relative abundance were tested at three spatial scales for multiple Lake Superior tributary streams. These spatial scales included the microhabitat (~1 m²), reach (50 m) and segment (2 km) spatial scale. Salmonid relative abundance was measured at microhabitat and reach scales via microhabitat visual surveys and reach electrofishing surveys. Thermal habitat characteristics were measured via standardized stream surveys at the microhabitat and reach scale and via GIS analyses at the segment scale. Use of GIS models and landscape spatial scale analyses generally performed well in locating potential flow pathways and areas of thermal refugia within a stream network. Most reaches containing predicted flow pathways exhibited a greater range in streamsubstrate interface and surface water temperatures than non-inflow reaches with multiple reaches contributing cold water to localized regions of a stream throughout the entire summer. Results of the best mixed linear effects models showed that salmonid relative abundance at the microhabitat scale was lower when surface water temperature was higher, higher when the temperature variation observed within a reach was higher and was higher stream segments had a higher density of predicted flow pathways. However, at all spatial scales, fixed thermal habitat effects used in mixed linear effects did not explain variations in salmonid relative abundance more than random effects. Though patterns of salmonid distribution and abundance within a stream network cannot be solely explained using thermal habitat characteristics, results of this study do suggest that preserving the thermal integrity of streams will help support healthy salmonid populations.

3.2 Introduction

Salmonids that inhabit the Lake Superior watershed can exhibit complex migratory and spawning behaviours (Holm et al., 2009; Robillard et al., 2011). Brook Trout, Rainbow Trout, Lake Trout, Brown Trout, Chinook Salmon, Coho Salmon and Pink Salmon have all been noted occupying Lake Superior tributary streams at varying times during a year (*Salvelinus fontinalis*; *Oncorhynchus mykiss*; *Salvelinus namaycush*; *Salmo trutta*; *Oncorhynchus tshawytscha*; *Oncorhynchus kisutch*; *Oncorhynchus gorbusha*; Holm et al., 2009). Among these species, only Brook Trout and Lake Trout are native to the Lake Superior watershed with all others being introduced (Holm et al., 2009). Brook Trout, Brown Trout, Coho Salmon, Chinook Salmon and Pink Salmon all spawn in streams during the late summer and fall (Holm et al., 2009). Though Lake Trout have been found occupying streams during the fall on rare occasions, streams are not spawning habitat for Lake Trout as they spawn in Lake Superior during the fall (Holm et al., 2009). Unlike other salmonids in the region, Rainbow Trout spawn in streams during the spring (Holm et al., 2009). Once juvenile salmonids emerge from their eggs, they will reside and grow in their natal tributary stream. Tributary streams provide a rich foraging habitat for juvenile salmonids due to the presence of high energy food sources and lack of predators (Miller & Sadro, 2003). The time an individual salmonid spends in its natal stream before migrating to larger body of water is known as residence time and varies among salmonid species and among individuals in a population (Miller & Sadro, 2003).

Stream resident ecotypes have been observed in some salmonid species (Jonsson, 1985; Robillard et al., 2011). Results from Robillard et al. (2011) supported the hypothesis that Brook Trout in the Lake Superior watershed exhibit two forms of migratory behaviour with a portion of the population staying in their natal streams (resident ecotype) and the other portion of the population eventually migrating into Lake Superior (lake ecotype). Analysis of Lake Superior resident and lake Brook Trout otoliths and vertebrae showed distinct differences in the growth, age of maturation and lifespan between the two hypothesized ecotypes. Lake ecotype Brook Trout generally grew and reached sexual maturity faster and lived longer compared to the stream ecotype (Robillard et al., 2011). For potamodromous salmonid species, such as the Brook Trout, streams can serve not only as a critical habitat for growing juveniles but also adult residents.

Salmonids are sensitive to ecological disturbances such as changes in water temperature and dissolved oxygen (Richter & Kolmes, 2005). The disturbance and fragmentation of salmonid habitat, along with stressors such as climate change and invasive species, has caused many salmonid populations to decline or become extirpated regionally (Marschall & Crowder, 1996;

Huckins et al., 2008). Lake Superior salmonid species, such as the Brook Trout, are socially, economically and environmentally valuable recreational fishes as well as good indicators of habitat quality in aquatic ecosystems due to the specific conditions required for their survival. Research and subsequent protection of salmonid critical habitat is essential in order to maintain, protect and restore Lake Superior salmonid populations.

One abiotic factor that is particularly important for salmonid survival is the availability of suitable thermal habitats (Baird & Krueger, 2003; Richter & Kolmes, 2005; Chu et al., 2008; Petty et al., 2012; Butryn et al., 2013). Salmonids are a cold-water fish and temperature regulates many of their physiological processes (Baird & Krueger, 2003; Richter & Kolmes, 2005; High et al., 2006; Butryn et al., 2013). Prolonged exposure to warm water can be lethal for cold-water fish (Baird & Krueger, 2003; Lund et al., 2003; Richter & Kolmes, 2005; Butryn et al. 2013). A commonly studied indicator of heat stress in animals is the expression of heat shock proteins which generally facilitate correct folding of new proteins as well as help refold proteins that become damaged by cell stress (Lund et al., 2003). Acute and chronic exposure of Brook Trout tissues to water temperature at or above 22°C yielded significant increases in the expression of heat shock proteins, indicating that water temperatures $\geq 22^{\circ}\text{C}$ induce a stress response in Brook Trout and may be limiting factor of Brook Trout abundance (Lund et al., 2003). In summer months, stream water temperatures may approach and surpass lethal levels for Brook Trout as well as other salmonid species. In these stressful conditions, individual salmonids must either avoid or adapt to warm water environments.

Multiple species of salmonid, such as Brook Trout, Rainbow Trout and Chinook Salmon, have been observed behaviourally thermoregulating by migrating and occupying localized regions of cold water within a watershed (Baird & Krueger, 2003; Ebersole et al., 2003; Goniea et al., 2006; High et al., 2006; Tiffan et al., 2009; Petty et al., 2012). Localized regions of cold water are often referred to as thermal refuges and serve as a critical habitat for many fish species. Past studies have shown salmonid distribution within stream network is influenced by the presence of localized regions of thermal refugia (Torgerson et al., 1999; Baird & Krueger, 2003; Ebersole et al., 2003; Petty et al., 2012).

Multiple abiotic factors influence the surface and substrate temperatures in streams. These factors include climate, stream flow, geology, morphology, land use and the condition of the canopy and riparian vegetation surrounding the stream (Poole & Berman, 2001; Chu et al., 2008). Surface and groundwater flow are two notable factors that can greatly influence water temperatures observed in streams by often adding cooler water to localized regions of a stream (Poole & Berman, 2001). Particularly in northern climates, surface runoff and groundwater

temperatures tend to be colder compared to stream water temperatures and thus often contribute colder water to a localized region of a stream (Poole & Berman, 2001). These regions of surface and groundwater flow can maintain consistently cool and stable thermal conditions within a watershed and serve as a thermal refugia for fish particularly during warm summer months (Poole & Berman, 2001; Baird & Krueger, 2003; Chu et al., 2008).

Streamflow can also greatly influence stream water temperatures (Poole & Berman, 2001; Chu et al., 2008). All stream discharge originates from precipitation which enters the stream directly through surface or groundwater flow (Poole & Berman, 2001). The pathway in which precipitation enters a stream is determined by land characteristics such as geology, topography and upland canopy and riparian vegetation (Poole & Berman, 2001). Streamflow is influenced by two components; base flow and stormflow (Smakhtin, 2001; Poole & Berman, 2001; Hodgkins & Dudley, 2011). Base flow is defined as the base level of streamflow that is sustained between precipitation events (Smakhtin, 2001; Hodgkins & Dudley, 2011). Stormflow is thus defined as the measured difference between total streamflow and base flow and represents increases in stream discharge due to short term precipitation events (Smakhtin, 2001; Hodgkins & Dudley, 2011). Particularly in northern climates like the Nipigon Bay, base flow conditions (or low flow conditions) are a seasonal phenomenon occurring during the summer months (June to September).

Anthropogenic influences such as climate change and land use activities can also alter the heat dynamics and temperature of stream habitats (Poole & Berman, 2001). Many anthropogenic influences, such as climate change, are expected to increase temperatures observed in streams (Poole & Berman, 2001; Mohseni et al., 2003; Chu et al., 2008). Climate-related increases in stream temperature will have profound implications for cold-water fishes and have the potential to decrease the amount of suitable thermal habitat, force northward shifts in the ranges of cold water fish, expose fish who cannot migrate due to physical barriers to more temperature stress as well as alter the quality and quantity of thermal refugia within a watershed (Mohseni et al., 2003; Chu et al., 2008).

Advances in technology, such as Geographic Information Systems (GIS), have improved the capability of researchers to study relationships between various habitat features observed at landscape spatial scales and fish ecology. One useful tool in GIS is the flow accumulation tool that can be used to predict the presence of thermal refugia at multiple locations along a stream. Since water flows in the direction of the steepest downhill gradient, water flow is influenced by the topography of the land as it flows downhill and accumulates in areas of low elevation (Kenny & Matthews, 2005). Flow accumulation tools in GIS map pathways of accumulating surface and groundwater flow by calculating the accumulated weight of all adjacent cells flowing into each

downslope cell (Kenny & Matthews, 2005). Using this tool, it is possible to predict locations where accumulated surface and shallow sub-surface flow enter the stream channel potentially creating thermal refuges for stream-dwelling fish. Flow accumulations appear in nature often as smaller stream channels flowing into a larger order stream or as wet patches along the stream bank that are shallow groundwater inputs.

In the past, the ecology of stream-dwelling fishes has been observed and studied at small spatial scales such as reaches and microhabitats (Fausch et al., 2002). However, most fisheries science methods, such as electrofishing and diver surveys, require immense amounts of time and effort which often limits the study of fish ecology to small spatial scales. Therefore, the study of fishes at landscape spatial scales are uncommon as the time, effort and travelling needed to survey larger spatial scales is often not feasible (Stanfield et al., 2006; Deschenes & Rodriguez, 2007). However, as processes such as climate change and urbanization occur on larger spatial scales, nested (or hierarchical) study designs that observe fish ecology at multiple spatial scales are becoming increasingly common (Torgerson et al., 1999; Fausch et al., 2002; Stanfield et al., 2006; Deschenes & Rodriguez, 2007).

My overall goal was to quantify relationships between salmonid abundance and stream thermal habitat characteristics observed at multiple spatial scales. These spatial scales included the microhabitat ($\sim 1 \text{ m}^2$), reach (50 m) and segment (2 km) scale. The first objective was to determine if stream reaches with inputs from flow accumulation pathways contained colder and more variable surface water and stream-substrate interface temperatures than non-flow pathway reaches. The second objective was to determine if thermal characteristics, such as stream-substrate interface temperature, surface temperature and substrate-stream temperature variation, explain the heterogeneity in salmonid relative abundance observed at a microhabitat scale. The third objective was to determine if thermal characteristics, such as surface temperature and substrate-stream temperature variation, explain the heterogeneity in salmonid relative abundance observed at a reach scale. The final objective was to determine if the number of predicted flow pathways entering the stream explains the heterogeneity in salmonid relative abundance observed at a reach scale.

3.3 Methods

For field data collection methods, refer to the General Methods section (1.3).

3.3.1 Data Analysis

Stream-substrate interface temperature variation was calculated as the difference between the coldest microhabitat stream-substrate interface temperature observed and mean microhabitat stream-substrate interface temperatures observed within the entire reach. Surface temperature variation was calculated as the difference between the coldest microhabitat surface temperature recorded during a given stream survey and mean microhabitat surface temperatures observed within the entire reach. Temperature variation measurements were separated into two groups: inflow and non-inflow reaches. A Wilcoxon signed rank test was also performed to test whether there was a significant difference in the temperature variation measurements observed between the two groups.

To study relationships between stream thermal habitat characteristics and salmonid relative abundance observed at multiple spatial scales, mixed linear effects models were used due to an unbalanced study design with nested observations. Modelling software used included the R (Version 3.5.3) with packages ‘lme4’ (mixed effects modelling) and ‘sjPlot’ (determination of random effects). Random intercept models and mixed linear effects models were used to study relationships between habitat characteristics observed at different spatial scales and salmonid relative abundance. Models were implemented using an array of random and fixed variables for each spatial scale (Table 3.1). Residual plots were made for all the best models to ensure models at each spatial scale contained normally distributed residuals.

Microhabitat scale mixed linear effects models utilized mean MaxN (mMaxN) estimates obtained from visual surveys and a combination of random effects (as intercept variables) and fixed effects (Table 3.2). The six random variables were stream sampled, date (Julian day), time (hour relative to 16:00), distance upstream from the mouth to Lake Superior (km), depth (m), and substrate type. The three fixed temperature variables were obtained from stream surveys and included stream-substrate interface temperature, surface temperature and substrate-surface temperature variation (calculated as the difference between microhabitat stream-substrate interface temperature and mean reach surface temperature). The best random effects models were determined by modelling every combination of random effects to determine the model with the lowest AICc value. Using the best random effects model, every combination of fixed effects was modelled. AICc values were calculated for each model to determine the best models. AICc values, deltaAICc, AICc weight and model likelihood were determined for the best random

effects models and the best three mixed effects models (combination of the best random and fixed effects).

Reach scale mixed linear effects models utilized salmonid catch-per-minute estimates from three-pass electrofishing surveys as well as visual surveys and a combination of random effects (as intercept variables) and fixed effects (Table 3.3). Because there was a significant relationship between reach mMaxN and catch-per-minute (Figure 2.3), I estimated reach catch-per-minute using the two microhabitat observations and the regression equation in order to generate replicate reach scale catch-per-minute:

$$\text{Catch-per-minute} = (\log(\text{mMaxN} + 1) + 0.05906) / 1.10432$$

The six random variables were stream sampled, date (Julian day), time (hour relative to 16:00), distance upstream from the mouth to Lake Superior (km), mean depth (m) and the dominant substrate type observed in the reach. The two fixed temperature variables calculated using temperature data loggers were surface temperature and substrate-surface temperature variation (calculated as the difference between cold microhabitat stream-substrate interface temperature and surface temperature). Best random effects models were determined by modelling every combination of random effects to determine the model with the lowest AICc value. Using the best random effects model, every combination of fixed effects was modelled. AICc values were calculated for each model to determine the best models. AICc values, deltaAICc, AICc weight and model likelihood were determined for the best random effects models and the best three mixed effects models (combination of the best random and fixed effects).

Segment scale mixed linear effects models utilized salmonid catch-per-minute data obtained from Upper Great Lakes Management Unit electrofishing surveys, catch-per-minute estimates used in the reach scale models and a combination of random effects (as intercept variables) and fixed effects (Table 3.4). Note that salmonid relative abundance and mean depth were measured at a reach spatial scale and that segment scale mixed linear effects models aimed to explain variation in salmonid relative abundance using landscape scale habitat characteristics. The five random variables were stream sampled, year, date (Julian day), time (relative to 16:00) and mean depth (m). The one fixed temperature variable used in stream scale analyses was the number of predicted flow pathways per kilometer. Predicted flow pathways per kilometer were determined using ArcGIS analysis of hydrology and the flow accumulation layers. For each surveyed stream, two kilometers of the stream, starting from the mouth, was traced using the trace feature and the number of flow pathways per stream segment was determined. All 2017 Dublin

Creek electrofishing surveys were removed from the stream scale analysis to ensure linear models contained normally distributed residuals. Best random effects models were determined by modelling every combination of random effects to determine the model with the lowest AICc value. Using the best random effect model, the influence of predicted flow pathways per segment on salmonid catch-per-minute was modelled. AICc values, deltaAICc, AICc weight and model likelihood were determined for the best random effects models and the only mixed effects model (combination of the best random and fixed effects).

3.4 Results

3.4.1 Temperature Variation Analyses

The stream-substrate interface temperature variation was significantly greater in inflow reaches than in non-inflow reaches ($V = 52$; $p < 0.05$; Figure 3.1). Similarly, the surface temperature variation was significantly greater in inflow reaches than in non-inflow reaches ($V = 36$; $p < 0.05$; Figure 3.2).

As stream surveys were only performed once during the study, recorded temperatures from temperature data loggers were used to observe changes in stream-substrate interface temperatures and surface temperatures occurring throughout the months of July and August (Figure 3.3). Air temperatures observed within the Nipigon Bay region were also gathered using historical weather data obtained from the Cameron Falls weather station (Figure 3.4). As inflow reaches generally contained microhabitats with the coldest stream-substrate interface temperatures, recorded temperatures at cold microhabitats were used to display the potential range in stream-substrate interface temperatures between cold microhabitat temperatures and stream surface temperatures. Substrate-surface temperature variation was substantial in Cypress River, Dublin Creek, East Ozone Creek and Roxy Creek. Substrate-surface temperature variation was less pronounced in Firehill Creek, Little Cypress River, Little Gravel River, MacInnes Creek, Ruby Creek and Wesley Creek.

3.4.2 Mixed Linear Effects Modelling

Microhabitat scale salmonid mMaxN-habitat models used data obtained through underwater camera surveys and stream surveys to determine the best random intercept and mixed effect models (Table 3.5). The best model was a random intercept model included the stream sampled (mean microhabitat mMaxN = 0.54). *Stream* was included as the random intercept effect used when running mixed effects models. The best mixed effects model included microhabitat surface temperature as a fixed effect and stream sampled as a random intercept effect and showed a negative linear relationship between surface temperature and salmonid mMaxN while accounting for the stream that was sampled (slope = -0.054; Figure 3.5). However, the best mixed effects model performed poorly in explaining the variation in salmonid relative abundance estimates and was 5.56 AICc units higher than the best random intercept model.

Reach scale salmonid catch-per-minute-habitat models used data obtained through underwater camera surveys, three-pass electrofishing surveys, stream surveys and recorded temperatures from temperature data loggers to determine the best random intercept and mixed effect models (Table 3.6). The best model was a random intercept model that included the stream sampled, date surveyed and mean reach depth (mean reach catch-per-minute = 0.37). *Stream, day,*

and *depth* were included as the random intercept effects used when running mixed effects models. The best mixed effects model included reach substrate-surface temperature variation as a fixed effect and stream sampled, date surveyed and mean reach depth as random intercept effects and showed a positive linear relationship between reach substrate-surface temperature variation and salmonid catch-per-minute accounting for *stream*, *day*, and *depth* (slope = 0.021; Figure 3.6). However, this mixed effects model performed poorly in explaining the variation in salmonid relative abundance estimates and was 8.26 AICc units higher than the best random intercept model.

Segment scale salmonid catch-per-minute-habitat models used data obtained through underwater camera surveys, three-pass electrofishing surveys, stream surveys and GIS analyses to determine the best random intercept and mixed effect models (Table 3.7). The best model was a random intercept model included the stream sampled and the year sampled (mean stream catchper-minute = 1.21). *Stream* and *year* were included as the random intercept effects used when running mixed effects models. The only mixed effects model at the segment scale included number of predicted flow pathways per segment as a fixed effect and stream sampled and year sampled as random intercept effects and showed a positive linear relationship between number of predicted flow pathways per segment and salmonid catch-per-minute accounting for *stream* and *year* (slope = 0.052; Figure 3.7). However, the best mixed effects model performed poorly in explaining the variation in salmonid relative abundance estimates and was 3.55 AICc units higher than the best random intercept model.

3.5 Discussion

Multiple predicted flow pathways did contribute colder water to a localized region within a reach as stream-substrate temperature variation was significantly higher in inflow reaches compared to non-inflow reaches. However, the magnitude of stream-substrate temperature variation among all studied inflow reaches varied. Stream-substrate temperature variation in some inflow reaches, such as the Cypress River, Dublin Creek, East Ozone Creek or Roxy Creek, was substantial. These reaches contained microhabitats with stream-substrate interface temperatures $\sim 7\text{-}9^{\circ}\text{C}$ colder relative to mean stream-substrate interface temperatures observed in the rest of the stream. However, in other predicted inflow reaches, stream-substrate temperature variation was minimal with two inflow reaches showing temperature variation of less than $\sim 1^{\circ}\text{C}$. Surface temperature variation was also significantly higher in inflow reaches compared to non-inflow reaches. However, compared to the wide range of stream-substrate interface temperatures that were observed within a given reach, differences in surface temperatures observed within a reach were minimal (mean reach surface temperature variation = 0.9°C).

Though GIS analyses generally performed well in predicting reaches that contained potential thermal refuges, these results must be interpreted with caution as thermal surveys often occurred at different times of day and on different dates. As shown in Figure 8, stream-substrate interface temperatures, surface temperatures and substrate-surface temperature variation are constantly changing daily, monthly and seasonally. During site selection performed from June 13 to July 5, all inflow reaches contained microhabitats of thermal refugia (microhabitats where the temperature at the stream-substrate interface was at least 1°C colder than the average substrate temperatures observed within the rest of the reach). By late July, the Little Cypress River, Little Gravel River and Ruby Creek reaches contained cold microhabitats with little substrate-surface temperature variation.

Results from temperature data loggers show notable reductions in reach substrate-surface temperature variation occurring particularly in the late summer (August). By late August, most studied reaches exhibited little substrate-surface temperature variation. However, inflow reaches in Cypress River, Dublin Creek, East Ozone Creek and Roxy Creek all maintained substantial substrate-surface variation throughout July and August. Diminishing temperature variation observed in previously thermally contributing inflow pathway reaches suggests a reduction in groundwater and surface flow that is characteristic of summer base flow conditions (Hodgkins et al., 2011). Temperature data obtained from the Cameron Falls weather station (closest weather station to Nipigon Bay) showed daily air temperatures reaching close to 30°C for multiple days in July and August. Though precipitation data could not be obtained from a weather station close to

the Nipigon Bay, recorded field observations and stream surveys suggest very few days of rain during the months of July and August. Hodgkins et al. (2011) studied summer base flow and stormflow trends for multiple New England rivers during 1950 to 2006 finding that air temperature and precipitation are key drivers of streamflow. The study observed that increases in stream base flows and stormflows observed at multiple automated hydrological stations were likely driven by the large increases in regional summer precipitation (Hodgkins et al., 2011). Seasonal patterns such as increasing summer air temperatures, increasing in stream evapotranspiration and decreasing monthly precipitation can be important drivers of streamflow and stream temperature dynamics and are likely responsible for the diminished temperature variation observed in multiple inflow reaches within the Nipigon Bay. For future studies, summer base flow conditions and precipitation should be considered when using predicted flow pathways to locate potential thermal refuges.

Microhabitat mixed effects models that used thermal microhabitat characteristics fit poorly compared to the best random intercept models. However, the best mixed effects model, which included the surface temperature as a fixed effect and the stream sampled as a random intercept effect, suggests a negative linear relationship between surface water temperatures and salmonid relative abundance. The relationship observed in the best mixed effects model is supported by past studies which have noted salmonid abundance and distribution within streams to be heavily influenced by stream water temperatures and the availability of thermal habitat (Torgerson et al., 1999; Baird & Krueger, 2003; Ebersole et al., 2003; Petty et al., 2012). In these studies, Brook Trout, Rainbow Trout and Chinook Salmon distribution and abundance increased in habitats containing colder water relative to mean water temperatures (Torgerson et al., 1999; Baird & Krueger, 2003; Ebersole et al., 2003; Petty et al., 2012). Higher salmonid relative abundance in microhabitats with colder surface water temperatures also supports the notion of salmonid behavioural thermoregulation (Torgerson et al., 1999; Baird & Krueger, 2003; Ebersole et al., 2003; Petty et al., 2012). Nipigon Bay salmonids may have migrated and occupied localized regions with relatively colder surface water to avoid temperature stress (Torgerson et al., 1999; Baird & Krueger, 2003; Ebersole et al., 2003; Petty et al., 2012).

Surface temperature was more influential as a fixed effect compared to substrate temperature even though stream survey results show surface temperature variation is minimal relative to stream-substrate interface temperature variation. During the summer, cold groundwater from the hyporheic zone of stream is constantly mixing with relatively warmer surface water that conforms to atmospheric temperatures (Poole & Berman, 2001). As water temperatures are often slightly colder closer to the stream substrate, one would expect stream-substrate interface

temperature to be a more influential habitat characteristic explaining heterogeneity in salmonid relative abundance observed at a microhabitat scale. Salmonid vertical distribution and movement within the water column varied among randomly subsampled minutes of video. However, salmonid vertical distribution patterns within studied microhabitats could not be explicitly tested because the size of individual salmonids captured in the video is unknown making vertical, horizontal and distal positions of fish difficult to measure given the methods used in the study. Based on observations made during video analysis, individual salmonids seemed to most often occupy the middle of the stream water column just slightly closer to the substrate.

Reach mixed effects models fit poorly compared to the best random intercept models. The best reach scale mixed effects models suggest a positive linear relationship between reach substrate-surface temperature variation and salmonid relative abundance. Past studies have noted a relationship between salmonid distribution and cold water thermal habitat characteristics observed at reach spatial scales (Torgerson et al., 1999; Baird & Krueger, 2003). GIS and landscape analyses generally performed well to predict and locate flow pathways within stream networks and generally flow pathway had higher thermal variability and thus contained more microhabitats that could be considered thermal refuges. However, reach scale thermal habitat features such as the thermal variability created by surface and subsurface water inputs associated with flow pathways did not influence salmonid relative abundance and distribution as much as expected.

Best reach models show little support for a net effect of mean reach depth explaining the heterogeneity in reach catch-per-minute. Mean reach depth generally had no net effect on salmonid relative abundance except the mean reach depth of 0.1 m which had a strong positive effect. However, results from the best reach models support a net positive effect between surveys performed at later dates in the summer and salmonid catch-per-minute. Except for two days, all days after Julian day 220 (August 8th) exerted a positive effect on reach relative abundance. As the random intercept effect of *date* yielded both the best fitting mixed effects as well as random intercept with fixed mean models, these results suggest salmonid abundance and distribution within a stream network changes throughout the summer.

Salmonid movements within stream networks have been a subject of great debate. Historically, stream fishes have been regarded as being sedentary; spending their entire lives confined to small habitats such as a single pool or a small stream reach (Gowan et al., 1994; Rodriguez, 2002). Observations of underwater videos, the suspected net positive effect of date surveyed and results of past studies suggest that the movement and movement behaviours of salmonids are more dynamic than previously thought (Kahler et al., 2001; Goniea et al., 2006;

Petty et al., 2012; Ecret & Mihuc, 2014). Salmonid size, genetic ecotype, seasonal patterns and the presence of thermal refuges have all been shown to influence the movement and distribution of salmonids within a stream network (Kahler et al., 2001; Goniea et al., 2006; Robillard et al. 2011; Petty et al., 2012; Ecret & Mihuc, 2014). Kahler et al. (2001) studied the movements of Coho Salmon, Rainbow Trout and cutthroat trout noting that 60% of marked fish did not stay in the same habitat over the summer and often would move into upstream habitats. Peterson & Fausch (2003) also studied the movements of nonnative Brook Trout and native cutthroat trout noting that nearly 80% of Brook Trout captured at studied weirs were moving upstream. Peterson & Fausch (2003) also noted that nearly 65% of cutthroat trout captured at studied weirs were moving downstream likely in response to the increased competition with Brook Trout in upstream habitats.

Salmonid movement behaviours observed in Kahler et al. (2001) and Peterson & Fausch (2003) may explain the net positive effect of survey date on salmonid catch-per-minute. One possible explanation for the net positive effect of survey date on salmonid relative abundance is that upstream movement behaviour is common among potamodromous species inhabiting the Nipigon Bay watershed. Surveys performed at later dates in the summer may have yielded a net positive effect on salmonid relative abundance because many individuals only managed to migrate to and occupy upstream habitats late in the summer. Therefore, a higher relative abundance of salmonids in reaches surveyed later in the summer may be due to an influx of salmonid competing for high quality microhabitats within a reach while a portion of salmonids continue migrating upstream in search of other high-quality unoccupied microhabitats.

Suspected upstream migration behaviours among Nipigon Bay salmonids could be influenced by stream scale temperature patterns (Torgersen et al., 1999). Torgersen et al. (1999) used thermal remote sensing methods to study stream temperature patterns at a reach spatial scale within John Day River basin in northeastern Oregon. They noted a general warming trend of reaches heading in the downstream direction (minus some cool and warm water anomalies). They also found that these stream scale temperature patterns appeared to be associated with major landscape features such as the presence of surface tributaries, groundwater inputs, valley morphology and stream canopy shading. Though some streams in arid climates are produced solely from surface runoff or stormflow, most streams originate from groundwater inputs (Poole & Berman, 2001). Therefore, the temperature of the groundwater input in which a stream channel originates is the original water temperature from which all water temperatures observed in the stream deviate (Poole & Berman, 2001). Generally, stream water temperature trends away from groundwater temperatures and trend towards air temperatures in a downstream direction (Poole &

Berman, 2001). During the summer months, groundwater temperatures in Lake Superior tributaries are likely colder than atmospheric temperatures at most times during a given day. Therefore, if stream temperature patterns in Nipigon Bay tributaries are like those observed by Torgerson et al. (1999), stream-dwelling salmonids may exhibit upstream movement behaviours as way of avoiding temperature stress by occupying upstream habitats that contain water temperatures closer to groundwater temperatures.

The best segment mixed effects and random intercept models suggest a weak net negative effect between surveys performed in recent years and salmonid catch-per-minute. Except for 2016 and 2017, all years post-2009 saw a negative effect of year surveyed on segment catch-per-minute. Though the best segment scale models suggest a decline in salmonid abundance within Lake Superior tributaries over the years, these results should be interpreted with caution due to very unbalanced sample size of segment survey data used to determine random intercept effects for each year.

The poor fit of the segment mixed effects model was somewhat unexpected as salmonid relative abundance was expected to be higher in streams with a higher number of predicted flow pathways within 2 km of the mouth of Lake Superior. In theory, a stream with a greater density of groundwater and surface flow pathways should provide more thermal refuges for cold-water fishes. A higher density of thermal refuges within a stream would be beneficial to resident stream-dwelling salmonid populations who would have more habitats available to avoid temperature stress. As prolonged exposure to warm water temperature can be lethal to an individual salmonid, streams that contain more thermal refuges should theoretically contain healthier and larger salmonid populations.

However, the poor fit of the segment scale mixed effect model likely occurred for two reasons. The first reason is that current methodologies are not very effective at estimating fish relative abundance at large spatial scales such as the watershed, stream or segment scale. Methods such as electrofishing and diver surveys require immense amounts of time and effort just to survey small portions of a stream. Very few researchers would have the time, effort or resources to perform an electrofishing or visual survey that could encompass an entire watershed or stream network. Most information concerning the relative abundance of fishes for an entire stream are based on observations and experiments conducted at smaller spatial scales such as the reach scale (often in locations that are easily accessible travelling on foot). The second reason is the potential limitation to the stream scale analyses and the set distance of 2 km that was defined as a stream segment. Depending on stream morphology, some smaller streams might only have a few kilometers of useable fish habitat where as a large stream such as the Cypress River has useable

fish habitat over a much greater distance. Since the amount of available stream habitat depends on stream size and discharge, the importance of landscape scale thermal habitat features for stream salmonids may be dependant on how much stream habitat is available.

Stream water temperatures change daily, monthly and seasonally and are influenced multiple factors. Multiple studies have suggested that the thermoregulatory behaviour of salmonids is influenced by daily, monthly and seasonal changes in stream water temperatures (Baird & Krueger, 2003; Ebersole et al., 2003; Goniea et al., 2006; High et al., 2006; Tiffan et al., 2009; Petty et al., 2012). Lake Superior tributaries, particularly Nipigon Bay tributaries, generally maintain cold water temperatures even during the summer months and thus are home to multiple species of cold-water fish. It was thought that salmonid distribution and relative abundance within a stream network would be clumped near predicted flow pathways that created cool thermal habitats during the warm summer months. However, if 20°C is considered the water temperature threshold in which most stream-dwelling salmonids begin to experience temperature stress, Nipigon Bay (Lake Superior) tributary streams are ideal salmonid habitat as surface temperature in most Nipigon Bay streams did not reach this 20°C threshold in the summer months of 2018. Surface temperature data loggers showed that only Cypress River, Dublin Creek and Firehill Creek consistently experienced surface water temperatures above 20°C. In all seven other streams studied, resident salmonids most likely did not experience temperature stress at any time during the summer (Lund et al. 2003; Butryn et al. 2013;). Theoretically, if an individual salmonid never experiences temperature stress during summer base flow conditions, that salmonid has no reason to prefer localized regions of thermal refugia. Therefore, if this individual has no need of thermal refuges, an observed clumped distribution of salmonids near predicted flow pathways would be unlikely because salmonids would likely not compete for food against multiple other individuals in a given habitat if they have the option to use a multitude of other unoccupied habitats.

Another possible explanation for not observing salmonid thermoregulatory behaviour concerns the limited dataset used in this study. The actual sampling of salmonids to generate relative abundance estimates occurred twice in one summer for most studied streams and thus this study obtained a glimpse into salmonid stream life over very short windows of time. Models used in this study accounted for potential differences in salmonid relative abundance across the dates and times in which field sampling occurred as random effects. However, it is still possible that behavioural thermoregulation was not observed at the reach scale because salmonid relative abundance was not measured at critical times during extremely warm days when salmonids would need to move and use thermal refuges to avoid temperature stress compared to the times relative abundance was observed in this study.

3.6 Tables and Figures

Table 3.1. Habitat variables at the microhabitat, reach and segment spatial scales used in mixed linear effects modelling.

<u>Spatial scale:</u>	<u>Random intercept variables:</u>	<u>Fixed variables:</u>
Microhabitat	<ul style="list-style-type: none"> • Stream • Date • Time • Distance upstream • Depth • Substrate type 	<ul style="list-style-type: none"> • Stream-substrate interface temperature • Surface temperature • Substrate-surface temperature
Reach	<ul style="list-style-type: none"> • Stream • Date • Time • Distance upstream • Mean depth • Dominant substrate type 	<ul style="list-style-type: none"> • Surface temperature • Substrate-surface temperature variation
Segment	<ul style="list-style-type: none"> • Stream • Year • Date • Time • Mean depth 	<ul style="list-style-type: none"> • Predicted flow pathways per segment

Table 3.2. Salmonid relative abundance (mMaxN) and habitat data used in microhabitat mixed effects models.

Site	mMaxN (RESPONSE)	Stream (RANDOM)	Julian day (RANDOM)	Hour relative to 16:00 (RANDOM)	Distance upstream (RANDOM)	Depth (RANDOM)	Substrate type (RANDOM)	Substrate temperature (FIXED)	Surface temperature (FIXED)	Temperature variation (FIXED)
Cypress_inflow_cold	0.043478	Cypress	192	2	2.355	0.29	Silt	13.2	19	3.3
Cypress_inflow_warm	0.347826	Cypress	192	2	2.365	0.1	Cobbles	22.8	22.8	-0.5
Cypress_noninflow_cold	1.043478	Cypress	192	-1	2.54	0.13	Cobbles	19	19.1	0.7
Cypress_noninflow_warm	1	Cypress	192	-1	2.585	0.08	Cobbles	20	20	-0.3
Dublin_inflow_cold	1.173913	Dublin	212	0	0.915	0.07	Silt	13	12	7.9
Dublin_inflow_warm	0.173913	Dublin	212	0	0.91	0.06	Cobbles	23	23.5	-2
Dublin_noninflow_cold	0.26087	Dublin	212	-4	1.055	0.03	Gravel	16.8	16.8	0.2
Dublin_noninflow_warm	0	Dublin	212	-4	1.015	0.08	Gravel	17.4	17	-0.4
Firehill_inflow_cold	0	Firehill	204	1	0.59	0.12	Silt	18	22.1	4.2
Firehill_inflow_warm	0.043478	Firehill	204	1	0.6	0.04	Silt	22.8	22.5	-0.6
Firehill_noninflow_warm	0	Firehill	200	-5	0.745	0.02	Silt	16.2	16.2	-0.1
Lilcypress_inflow_cold	0.26087	LittleCypres	205	1	0.635	0.13	Silt	15.5	17.1	1.7
Lilcypress_inflow_warm	0.608696	LittleCypres	205	1	0.65	0.01	Cobbles	21.4	19.1	-4.2
Lilcypress_noninflow_cold	0.565217	LittleCypres	205	-3	0.47	0.14	Silt	14.6	14.9	0.3
Lilcypress_noninflow_warm	0	LittleCypres	205	-3	0.455	0.29	Silt	15.3	15	-0.4
Lilgravel_inflow_cold	1	LittleGravel	214	0	1.455	0.11	Silt	13.7	15.7	2.1
Lilgravel_inflow_warm	0.043478	LittleGravel	214	0	1.48	0.06	Cobbles	15.9	16.1	-0.1
Lilgravel_noninflow_cold	0.826087	LittleGravel	214	-3	1.255	0.06	Silt	11.9	13.5	1.9
Lilgravel_noninflow_warm	0.173913	LittleGravel	214	-3	1.235	0.5	Silt	14.2	13.9	-0.4
MacInnes_inflow_cold	0.217391	MacInnes	206	1	1.465	0.41	Silt	12.7	14	1.4
MacInnes_inflow_warm	2.782609	MacInnes	206	1	1.49	0.26	Boulders	14.4	14.4	-0.3
MacInnes_noninflow_cold	1.391304	MacInnes	206	-4	1.255	0.15	Boulders	12.6	13.1	0.6
MacInnes_noninflow_warm	2.608696	MacInnes	206	-4	1.21	0.13	Silt	13.9	13.4	-0.7
Roxy_inflow_cold	0	Roxy	213	-2	1.75	0.11	Silt	5.7	13.5	8.5
Roxy_inflow_warm	0	Roxy	213	-2	1.73	0.13	Silt	14.8	14.3	-0.6
Roxy_noninflow_cold	0	Roxy	211	-1	1.86	0.54	Silt	12.8	14.7	2
Roxy_noninflow_warm	0	Roxy	211	-1	1.91	0.55	Bedrock	14.7	14.8	0.1
Ruby_inflow_cold	0	Ruby	198	1	0.945	0.12	Silt	14.1	15.5	1.4
Ruby_inflow_warm	0.043478	Ruby	198	1	0.98	0.2	Silt	15.6	15.6	-0.1
Ruby_noninflow_cold	0.043478	Ruby	198	-5	1.095	0.5	Silt	13.6	14.5	1
Ruby_noninflow_warm	0	Ruby	198	-5	1.07	0.29	Silt	15	14.5	-0.4
Wesley_inflow_cold	0.304348	Wesley	221	-2	0.935	0.06	Silt	10.4	10.4	1
Wesley_inflow_warm	3.217391	Wesley	221	-2	0.95	0.03	Cobbles	11.7	11.5	-0.3
Wesley_noninflow_cold	0.304348	Wesley	220	-4	0.835	0.24	Silt	10	10.3	0.2
Wesley_noninflow_warm	0.608696	Wesley	220	-4	0.81	0.19	Silt	10.9	10.5	-0.7

Table 3.3. Salmonid catch-per-minute and habitat data used in reach mixed linear effects models. Site names ending with an “E” denote catch-per-minute estimates obtained through three-pass electrofishing surveys and site names that do not end with an “E” denote catch-per-minute estimates obtained using mean salmonid mMaxN from two microhabitat within each reach.

Site	CPM (RESPONSE)	Stream (RANDOM)	Julian day (RANDOM)	Hour relative to 16:00 (RANDOM)	Distance upstream (RANDOM)	Dominant substrate type (RANDOM)	Mean depth (RANDOM)	Surface temperature (FIXED)	Temperature variation (FIXED)
Cypress_inflowE	0.53584	Cypress	225	1	2.33	Boulders	0.3	26.1	12.2
Cypress_noninflowE	0.28249	Cypress	226	-5	2.54	Cobbles	0.26	20.1	0.7
Dublin_inflowE	0.62208	Dublin	227	-2	0.89	Boulders	0.21	21.2	8.1
Dublin_noninflowE	0.41654	Dublin	227	-5	1.01	Cobbles	0.13	16.8	0.3
EastOzone_inflowE	1.12514	EastOzone	230	-1	0.22	Cobbles	0.13	15.3	3.8
EastOzone_noninflow	2.21733	EastOzone	230	-5	0.36	Cobbles	0.1	13.2	0
Firehill_inflowE	0.04181	Firehill	227	1	0.57	Silt	0.07	21.6	0
Firehill_noninflowE	0.15534	Firehill	228	-6	0.72	Cobbles	0.12	14.2	0
Lilypress_inflowE	0.24908	LittleCypress	226	0	0.6	Cobbles	0.16	17.4	0.1
Lilypress_noninflowE	0.17595	LittleCypress	226	-1	0.45	Cobbles	0.14	17.1	0
MacInnes_inflowE	0.86957	MacInnes	229	0	1.44	Cobbles	0.2	14.8	1.8
MacInnes_noninflowE	0.73142	MacInnes	229	-3	1.21	Cobbles	0.12	13.7	0.4
Roxy_inflowE	0.01775	Roxy	231	-5	1.73	Silt	0.19	15.9	3.8
Roxy_noninflowE	0.04835	Roxy	231	-4	1.86	Silt	0.24	16	0.4
Ruby_inflowE	0.21958	Ruby	228	0	0.94	Silt	0.25	16.4	0
Ruby_noninflowE	0.19491	Ruby	228	-2	1.05	Silt	0.37	15.3	0.4
Cypress_inflow	0.12375	Cypress	192	2	2.33	Boulders	0.3	22.5	8.5
Cypress_noninflow	0.33033	Cypress	192	-1	2.54	Cobbles	0.26	23.7	0.7
Dublin_inflow	0.25608	Dublin	212	0	0.89	Boulders	0.21	22.3	7.8
Dublin_noninflow	0.10170	Dublin	212	-4	1.01	Cobbles	0.13	18.6	0.5
Firehill_inflow	0.06194	Firehill	204	1	0.57	Silt	0.07	21.5	0
Firehill_noninflow	0.05348	Firehill	200	-5	0.72	Cobbles	0.12	19.5	3
LittleCypress_inflow	0.19546	LittleCypress	205	1	0.6	Cobbles	0.16	17.8	0
LittleCypress_noninflow	0.15136	LittleCypress	205	-3	0.45	Cobbles	0.14	16.1	0.2
LittleGravel_inflow	0.21860	LittleGravel	219	0	1.43	Cobbles	0.2	17	0.5
LittleGravel_noninflow	0.21294	LittleGravel	219	-3	1.22	Silt	0.19	15.6	0.8
MacInnes_inflow	0.41383	MacInnes	206	1	1.44	Cobbles	0.2	15.7	0.9
MacInnes_noninflow	0.48553	MacInnes	206	-4	1.21	Cobbles	0.12	14.4	0.6
Roxy_inflow	0.05348	Roxy	213	-2	1.73	Silt	0.19	14.4	5.8
Roxy_noninflow	0.05348	Roxy	211	-1	1.86	Silt	0.24	14.5	0
Ruby_inflow	0.06194	Ruby	198	1	0.94	Silt	0.25	16.7	0.2
Ruby_noninflow	0.06194	Ruby	198	-5	1.05	Silt	0.37	14.6	0
Wesley_inflow	0.45286	Wesley	221	-2	0.91	Cobbles	0.19	15.4	2.9
Wesley_noninflow	0.20136	Wesley	220	-4	0.79	Cobbles	0.15	11.1	0.1

Table 3.4. Salmonid catch-per-minute and habitat data used in segment mixed linear effects models.

Site	CPM (RESPONSE)	Stream	Year	Julian Day	Hour relative to 16:00	Mean depth	Flow pathways / segment
Mcint1	1.82375	McIntyre	2000	242	-2	0.12	2.5
Mcint2	2.03655	McIntyre	2000	243	-2	0.12	2.5
Mcint3	0.69220	McIntyre	2000	249	-4	0.15	2.5
Mcint4	3.07261	McIntyre	2001	204	-2	0.15	2.5
Mcint5	4.20163	McIntyre	2001	205	-1	0.14	2.5
Mcint6	1.01942	McIntyre	2001	206	-3	0.11	2.5
Mcint7	0.73657	McIntyre	2001	207	-3	0.11	2.5
Mcint8	4.60667	McIntyre	2003	210	-2	0.16	2.5
Mcint9	6.88746	McIntyre	2003	215	-3	0.1	2.5
Mcint10	1.47148	McIntyre	2003	217	-3	0.15	2.5
Mcint11	0.12238	McIntyre	2003	219	-3	0.12	2.5
Mcint12	5.60173	McIntyre	2003	220	-2	0.15	2.5
Mcint13	3.44942	McIntyre	2004	257	-3	0.16	2.5
Mcint14	3.40164	McIntyre	2004	258	-3	0.16	2.5
Mcint15	1.49394	McIntyre	2009	189	-1	0.19	2.5
Ferg1	0.15686	Ferguson	2009	225	-4	0.16	3.5
Ferg2	0.23873	Ferguson	2009	225	-1	0.24	3.5
Ferg3	0.48837	Ferguson	2009	226	-5	0.13	3.5
Crad1	0.06547	Craddock	2009	229	-2	0.14	2.5
Crad2	0.07958	Craddock	2009	229	-5	0.13	2.5
Crad3	0.00000	Craddock	2009	230	-6	0.11	2.5
Mcint16	2.56030	McIntyre	2009	222	-2	0.14	2.5
Mcint17	0.85930	McIntyre	2009	223	-1	0.1	2.5
Mcint18	1.14333	McIntyre	2009	224	-2	0.15	2.5
Crad4	0.17304	Craddock	2010	208	-3	0.09	2.5
Crad5	0.05277	Craddock	2010	209	-3	0.07	2.5
Crad6	0.18496	Craddock	2010	209	-6	0.1	2.5
Ferg4	0.23560	Ferguson	2010	210	-6	0.09	3.5
Ferg5	0.88059	Ferguson	2010	210	-3	0.1	3.5
Mcint19	2.67644	McIntyre	2010	251	-1	0.1	2.5
Ferg6	1.50129	Ferguson	2011	209	-6	0.1	3.5
Ferg7	0.03579	Ferguson	2011	209	-5	0.4	3.5
Ferg8	0.41451	Ferguson	2011	209	-4	0.15	3.5
Mcint20	2.03959	McIntyre	2011	237	-5	0.1	2.5
Ferg9	0.71535	Ferguson	2012	233	-4	0.33	3.5
Ferg10	0.64188	Ferguson	2012	233	-2	0.5	3.5
Ferg11	0.60120	Ferguson	2012	233	-1	0.5	3.5
Crad7	0.05254	Craddock	2012	234	-5	0.33	2.5
Crad8	0.00000	Craddock	2012	234	-7	0.33	2.5
Crad9	0.15983	Craddock	2012	234	-2	0.5	2.5
Mcint21	0.63993	McIntyre	2012	235	-6	0.25	2.5
Mcint22	0.06061	McIntyre	2012	236	-5	0.25	2.5
Mcint23	0.40483	McIntyre	2012	236	-2	0.25	2.5
Mevic1	0.78161	McVicars	2012	244	-6	0.2	2
Mevic2	1.32879	McVicars	2012	244	-5	0.3	2
Mevic3	1.88849	McVicars	2012	244	-3	0.35	2
Mcint24	0.22460	McIntyre	2014	225	-5	0.2	2.5
Mcint25	1.50000	McIntyre	2014	225	-1	0.14	2.5

Site	CPM (RESPONSE)	Stream	Year	Julian Day	Hour relative to 16:00	Mean depth	Flow pathways / segment
Mcint26	0.91324	McIntyre	2014	225	-3	0.17	2.5
Mcint27	0.51873	McIntyre	2014	226	-2	0.14	2.5
Mcint28	1.30178	McIntyre	2014	227	-7	0.15	2.5
Port1	1.78660	Portage	2014	240	-5	0.15	3
Port2	1.36882	Portage	2014	240	-3	0.3	3
Mcint29	1.00784	McIntyre	2015	202	-1	0.22	2.5
Mcint30	1.54286	McIntyre	2015	202	-7	0.19	2.5
Mcint31	2.81946	McIntyre	2015	202	-6	0.19	2.5
Mcint32	2.06009	McIntyre	2015	203	-7	0.17	2.5
Mcint33	0.22936	McIntyre	2015	211	-2	0.22	2.5
Mcint34	0.15075	McIntyre	2015	212	-6	0.22	2.5
Black1	0.04918	Black	2015	223	-3	0.1	4
Stok1	0.11278	Stokely	2015	223	-5	0.15	1.5
Gov1	0.39978	Government	2015	224	-1	0.15	6.5
Alob1	0.30483	Alona	2015	225	-5	0.4	3
Rob1	0.33333	Robertson	2015	229	-1	0.2	1.5
Spect1	0.57592	Speckled	2015	230	-2	0.1	4
Sand1	0.21871	Sand	2015	233	-3	0.8	3.5
Barr1	0.09934	Barrett	2015	238	-4	0.2	4.5
Mcint35	1.67247	McIntyre	2016	221	-2	0.12	2.5
Mcint36	2.48848	McIntyre	2016	221	-5	0.13	2.5
Mcint37	1.72205	McIntyre	2016	225	-7	0.12	2.5
Mcint38	2.31203	McIntyre	2016	225	-4	0.16	2.5
Mcint39	1.80000	McIntyre	2016	227	-6	0.15	2.5
Mcint40	2.11429	McIntyre	2017	208	-3	0.15	2.5
Mcint41	2.08421	McIntyre	2017	209	-5	0.2	2.5
Mcint42	1.54748	McIntyre	2017	209	-4	0.14	2.5
Mcint43	1.98773	McIntyre	2017	209	-2	0.16	2.5
Blen1	5.14955	Blende	2017	212	-3	0.25	3
Sib1	1.32597	Sibley	2017	212	-4	0.18	2.5
Joe	0.00000	Joeboy	2017	214	-7	0.07	1
Sib2	2.65139	Sibley	2017	214	-5	0.45	2.5
Port3	2.67050	Portage	2017	215	-4	0.18	3
Port4	0.97035	Portage	2017	215	-2	0.37	3
Ferg12	0.09600	Ferguson	2017	216	-7	0.25	3.5
Ferg13	1.13402	Ferguson	2017	216	-6	0.29	3.5
Ferg14	0.62827	Ferguson	2017	216	-5	0.35	3.5
Unkn1	2.83727	Unknown	2017	220	-5	0.16	2.5
Unkn2	5.96195	Unknown	2017	220	-3	0.26	2.5
Boul1	0.00000	Boulter	2017	226	-5	0.25	3.5
Cold1	1.72485	Coldwater	2017	227	-4	0.16	2
Morr1	0.00000	Morrow	2017	227	-2	0.24	1.5
Neys1	1.11940	Neys	2017	228	2	0.19	1.5
Neys2	2.38698	Neys	2017	228	2	0.14	1.5
Angler1	0.00000	Angler	2017	229	-5	0.14	1
Crad10	0.00000	Craddock	2017	229	-1	0.11	2.5
Neys3	3.62869	Neys	2017	229	-9	0.16	1.5
Neys4	1.59858	Neys	2017	229	-7	0.15	1.5
Unkn3	6.63934	Unknown	2017	230	-4	0.12	2.5
Litg1	1.43012	Littlegravel	2017	233	-2	0.73	1.5
Nish1	0.00000	Nishin	2017	233	-3	0.06	3.5

Site	CPM (RESPONSE)	Stream	Year	Julian Day	Hour relative to 16:00	Mean depth	Flow pathways / segment
Cypress_inflowE	0.53584	Cypress	2018	225	1	0.3	1
Cypress_noninflowE	0.28249	Cypress	2018	226	-5	0.26	1
Dublin_inflowE	0.62208	Dublin	2018	227	-2	0.21	3.5
Dublin_noninflowE	0.41654	Dublin	2018	227	-5	0.13	3.5
EastOzone_inflowE	1.12514	EastOzone	2018	230	-1	0.13	3.5
EastOzone_noninflowE	2.21733	EastOzone	2018	199	-5	0.1	3.5
Firehill_inflowE	0.04181	Firehill	2018	227	1	0.07	1.5
Firehill_noninflowE	0.15534	Firehill	2018	228	-6	0.12	1.5
Lilcypress_inflowE	0.24908	LittleCypress	2018	226	0	0.16	2
Lilcypress_noninflowE	0.17595	LittleCypress	2018	226	-1	0.14	2
MacInnes_inflowE	0.86957	MacInnes	2018	229	0	0.2	4
MacInnes_noninflowE	0.73142	MacInnes	2018	229	-3	0.12	4
Roxy_inflowE	0.01775	Roxy	2018	231	-5	0.19	2
Roxy_noninflowE	0.04835	Roxy	2018	231	-4	0.24	2
Ruby_inflowE	0.21958	Ruby	2018	228	0	0.25	2
Ruby_noninflowE	0.19491	Ruby	2018	228	-2	0.37	2
Cypress_inflow	0.12375	Cypress	2018	192	2	0.3	1
Cypress_noninflow	0.33033	Cypress	2018	192	-1	0.26	1
Dublin_inflow	0.25608	Dublin	2018	212	0	0.21	3.5
Dublin_noninflow	0.10170	Dublin	2018	212	-4	0.13	3.5
Firehill_inflow	0.06194	Firehill	2018	204	1	0.07	1.5
Firehill_noninflow	0.05348	Firehill	2018	200	-5	0.12	1.5
LittleCypress_inflow	0.19546	LittleCypress	2018	205	1	0.16	2
LittleCypress_noninflow	0.15136	LittleCypress	2018	205	-3	0.14	2
LittleGravel_inflow	0.21860	LittleGravel	2018	214	0	0.2	1.5
LittleGravel_noninflow	0.21294	LittleGravel	2018	214	-3	0.19	1.5
MacInnes_inflow	0.41383	MacInnes	2018	206	1	0.2	4
MacInnes_noninflow	0.48553	MacInnes	2018	206	-4	0.12	4
Roxy_inflow	0.05348	Roxy	2018	213	-2	0.19	2
Roxy_noninflow	0.05348	Roxy	2018	211	-1	0.24	2
Ruby_inflow	0.06194	Ruby	2018	198	1	0.25	2
Ruby_noninflow	0.06194	Ruby	2018	198	-5	0.37	2
Wesley_inflow	0.45286	Wesley	2018	221	-2	0.19	3
Wesley_noninflow	0.20136	Wesley	2018	220	-4	0.15	3

Table 3.5 Best salmonid microhabitat mixed linear effects models explaining the heterogeneity in microhabitat mMaxN.

Random effects	Fixed effects	deltaAICc	AICc weight	Model likelihood
Stream	(None)	0.0000	0.2663	1.0000
Date	(None)	0.2572	0.2342	0.8793
Substrate type	(None)	0.4335	0.2144	0.8051
Stream + subtype type	(None)	1.2482	0.1427	0.5358
Stream + distance	(None)	1.2523	0.1424	0.5347
Date + distance	(None)	1.5639	0.1218	0.4575
Date + substrate type	(None)	1.7133	0.1131	0.4246
Distance + substrate type	(None)	1.8145	0.1075	0.4036
Stream	Surface temperature	5.5560	0.0166	0.0622
Stream	Temperature variation	6.5483	0.0101	0.0378
Stream	Substrate temperature	7.1220	0.0076	0.0284

Table 3.6 Best salmonid reach mixed linear effects models explaining the heterogeneity in reach catch-per-minute.

Random effects	Fixed effects	deltaAICc	AICc weight	Model Likelihood
Stream + date + depth	(None)	0.0000	0.4165	1.0000
Stream	(None)	0.0930	0.3976	0.9546
Stream + date + distance	(None)	1.6877	0.1791	0.4300
Stream + date + depth	Thermal variability	8.2567	0.0067	0.0161
Stream + date + depth	Surface Temperature	9.1370	0.0043	0.0104
Stream + date + depth	Thermal variability + surface temperature	17.1304	0.0001	0.0002

Table 3.7 Best salmonid segment mixed linear effects models explaining the heterogeneity in reach catch-per-minute.

Random effects	Fixed effects	deltaAICc	AICc weight	Model Likelihood
Stream + year	(None)	0.0000	0.6577	1.0000
Stream + year + depth	(None)	2.0944	0.2308	0.3509
Stream + year	Flow pathways / segment	3.5500	0.1115	0.1695

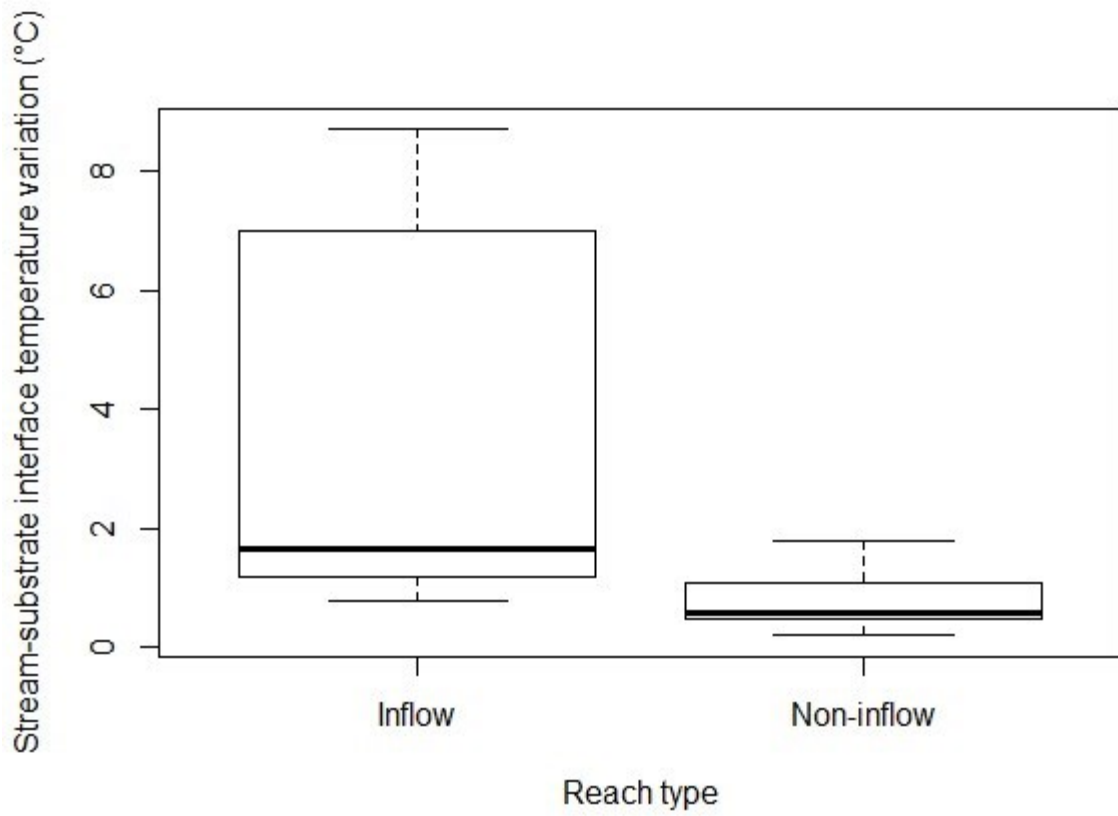


Figure 3.1. Substrate-stream interface temperature variation measured at inflow and non-inflow reaches during stream survey

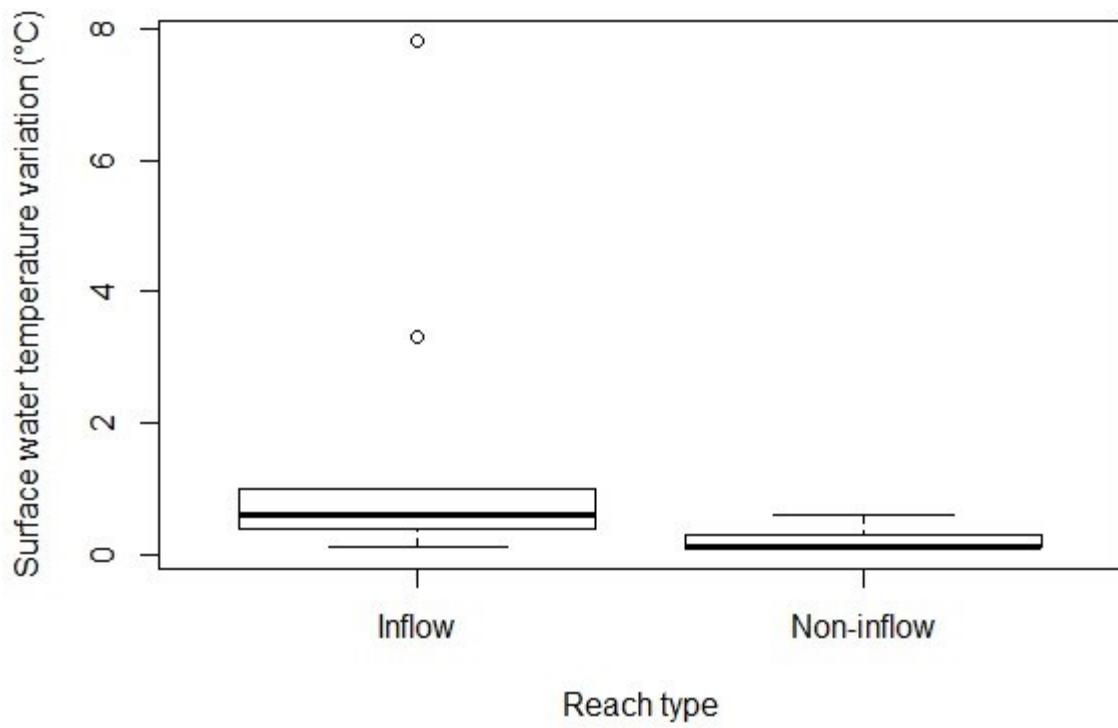


Figure 3.2. Surface water temperature variation measured at inflow and non-inflow reaches during stream surveys.

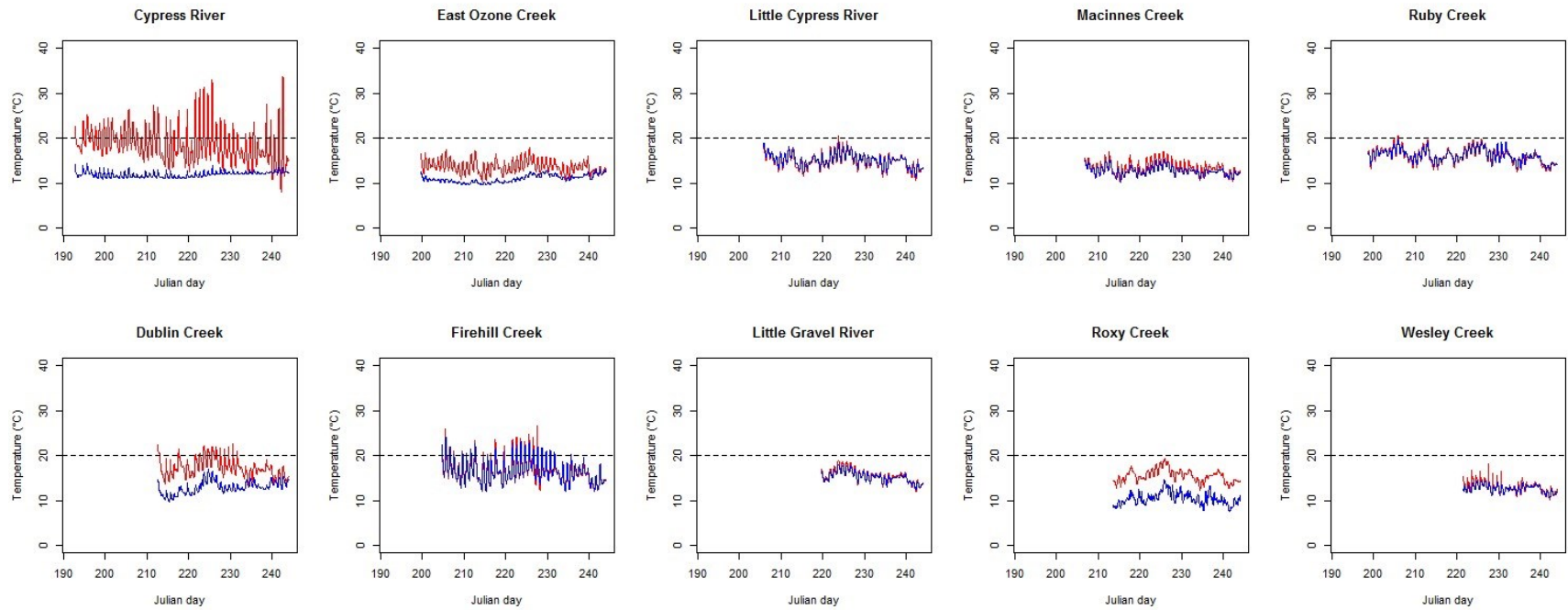


Figure 3.3. Stream temperatures measured during July and August (2018). Red lines are stream surface temperatures and blue lines are stream-substrate interface temperatures observed at the “cold” microhabitat within the “inflow” reach. Dashed black lines show a temperature threshold of 20°C (roughly the temperature salmonids like the Brook Trout are supposed to experience temperature stress).

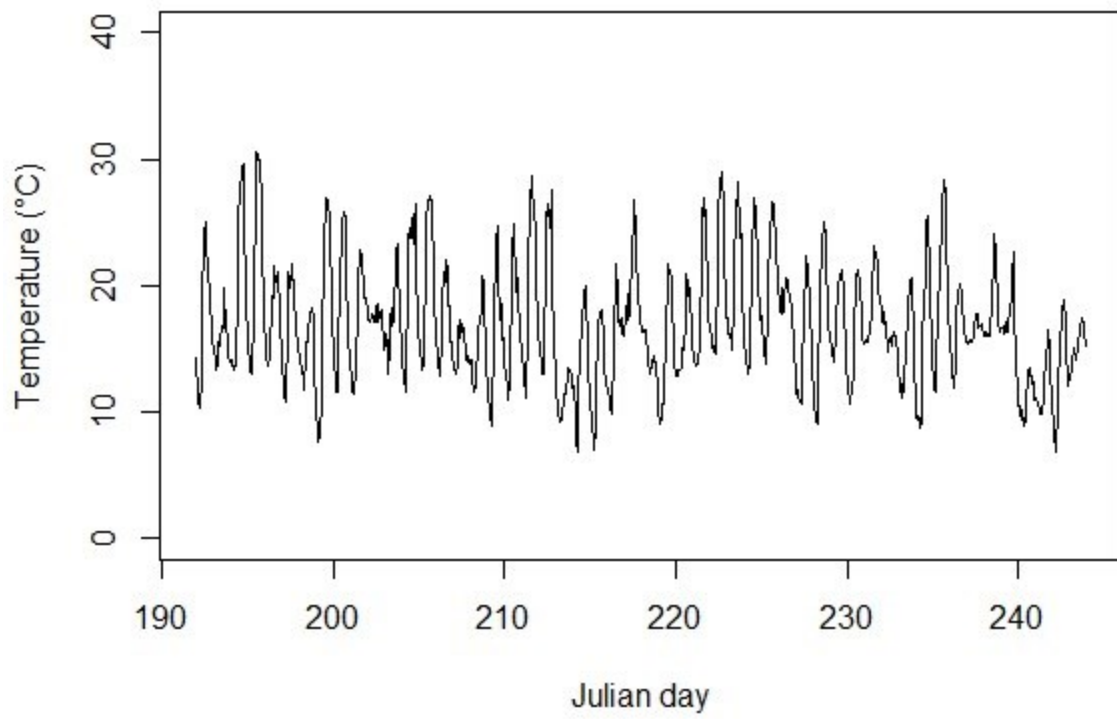
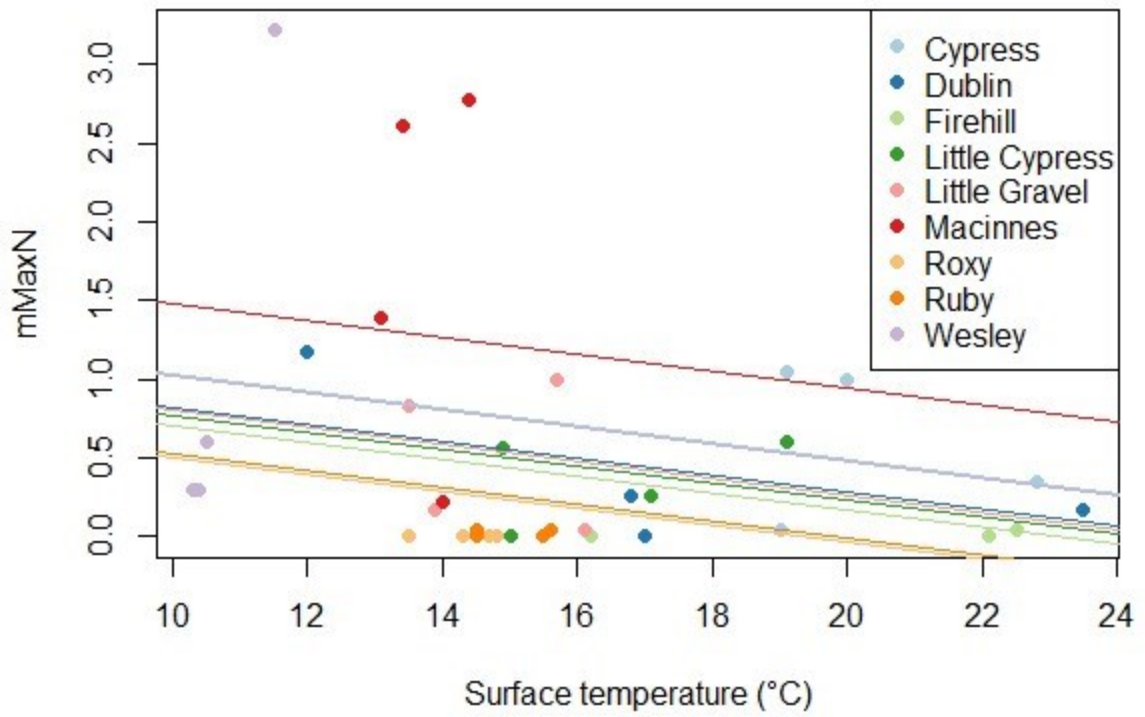


Figure 3.4. Hourly air temperature measured at the Cameron Falls weather station during July and August (2018).



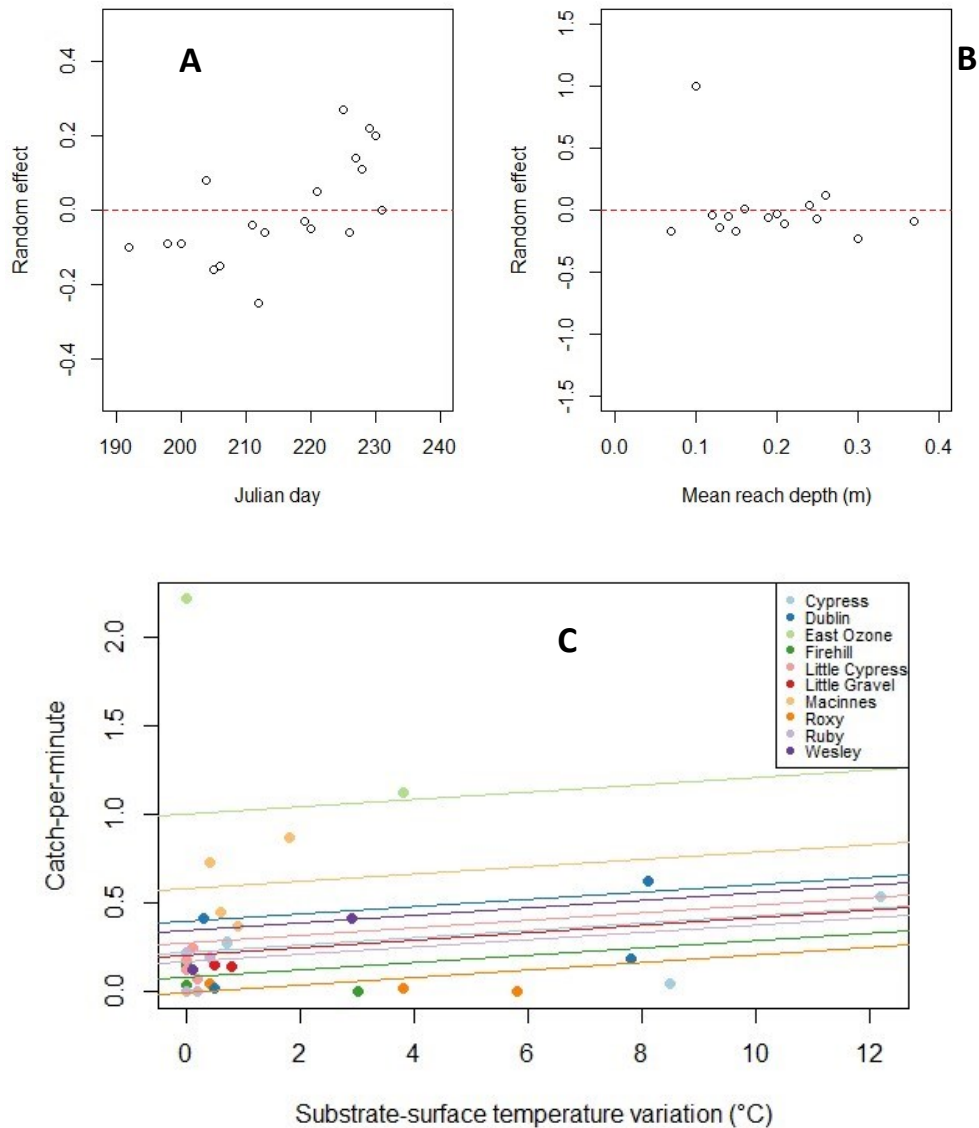


Figure 3.6. Visual representation of the best reach fixed effects model which included reach thermal variability as a fixed effect and stream sampled, date surveys occurred and mean reach depth as random intercept effects. Panel A shows the random intercept effects of Julian day on salmonid catch-per-minute. Panel B shows the random intercept effects of mean reach depth on salmonid catch-per-minute. Coloured dots in panel C show salmonid catch-per-minute in reaches that range in substrate-surface temperature variation. Coloured lines in panel C show the calculated regression lines of the reach catch-per-minute-substrate-surface temperature variation relationship \pm the random intercept effect of the stream sampled.

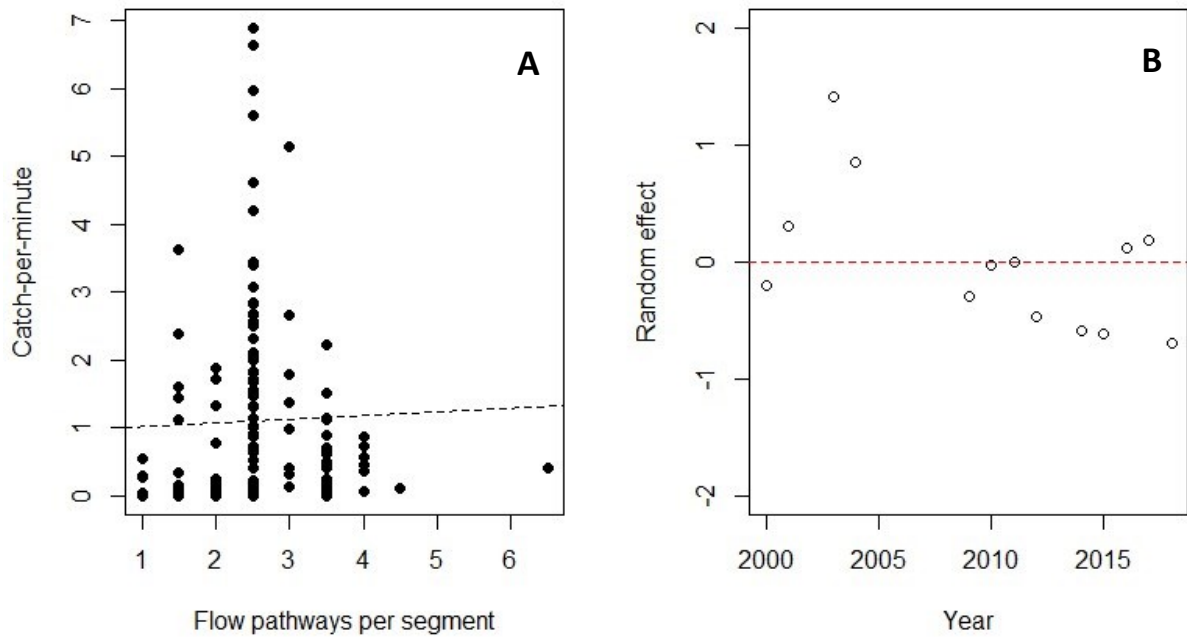


Figure 3.7. Visual representation of the segment fixed effects model which included the number of predicted flow pathways as a fixed effect and stream sampled and year sampled date surveys as random intercept effects. Dots in Panel A show salmonid catch-per-minute in streams that range in the number of flow pathways predicted to occur within a 2km segment starting at the mouth of Lake Superior. Note that coloured lines showing the calculated regression lines of the reach catch-per-minute-substrate-flow pathway per segment relationship \pm the random intercept effect of the stream sampled were not displayed due to a limited palette of colours. Panel B shows the random intercept effects of year sampled on salmonid catch-per-minute.

Chapter 4. Conclusion

Results from this study showed significant relationships in estimates salmonid relative abundance obtained using visual and traditional (electrofishing) methods further supporting the use of unbaited underwater cameras to generate reliable measurements of fish relative abundance. Unbaited underwater camera methods show potential serving as a viable alternative to traditional fisheries methods to study fish habitat relationships at varying spatial scales. Underwater cameras do not harm fish and are well-suited for the study of fishes at microhabitat spatial scales. Additionally, visual survey methods are considered less likely to alter fish behaviour compared to methods such as electrofishing. Fish observed in the underwater video displayed no noticeable curiosity or avoidance of either the camera or tripod. This makes the unbaited camera methods presented ideal to study of fish microhabitat preference and behaviours because the presence of underwater cameras is unlikely to alter fish behaviour and movements.

Another advantage associated with the visual survey methods used in this study is that camera gear (even a remotely operated vehicle to some extent) generally weighs less than electrofishing gear. The portability and light weight of many visual survey methods can allow for smaller field crews as less effort is needed to carry gear into remote field sites. The added mobility of using camera gear (compared to other traditional methods) would especially be of benefit when studying stream ecology at larger spatial scales such as the segment, stream and watershed spatial scales.

High levels of variation between salmonid microhabitat relative abundance (mMaxN) estimates and salmonid reach relative abundance (catch-per-minute) estimates were observed likely due to the substantial variation in salmonid distribution and abundance that can occur at different microhabitats within a reach. Improved unbaited camera methods which account for potential high variations in salmonid microhabitat relative abundance would be needed in order to precisely estimate fish relative abundance at larger spatial scales. Use of distance sampling concepts (e.g. point sampling concepts), standardized camera placement methods and more camera replicates could help researchers obtain relative abundance estimates at large spatial scale that accurately represent the true abundance of fish inhabiting that spatial scale.

Stream temperature results obtained via stream surveys and temperature data loggers showed that the quality, size and persistence of thermal refugia created by surface and subsurface water inputs varied. With that said, use of GIS models generally performed well in locating potential flow paths and areas of thermal refugia within a

stream network. Most inflow reaches exhibited a greater range in stream-substrate interface and surface temperatures than non-inflow reaches with a few inflow reaches having persistent cold water areas in localized regions of streams even in late August (peak base flow conditions). Landscape scale methods used in this study also make for a less time-consuming method in locating thermal refuges within a stream, as traditional methods for locating localized regions of thermal refugia generally require more on foot travel and field validation. However, summer base flow conditions brought on by warmer air temperatures and decreases in seasonal precipitation should be considered when using a GIS to locate potential localized regions of thermal refugia as the thermal quality of many flow pathway reaches diminished by the late summer.

Fixed effects models that included Lake Superior thermal habitat characteristics did not explain variations in salmonid relative abundance compared to random intercept with fixed mean models. These results were unexpected because previous research of salmonid thermoregulatory behaviour suggests that the distribution and relative abundance of stream-dwelling salmonids is heavily influenced by water temperatures with individuals clumping to the coldest habitat that is available to them. However, Nipigon Bay tributary streams experienced a summer with relatively cold air temperatures. Of the 10 studied streams, only three experienced surface water temperatures consistently above 20°C. Future research into salmonids thermal habitat use (or lack of use) at multiple spatial scales, should consider mixed effects modelling methods used in this study as the use of random effects (such as the stream, date and year surveyed) can help further our understanding of the ecological factors which contribute to variations in fish abundance observed at different spatial scales.

Results from this study also support the notion that salmonid distribution and movements within a stream network change in response to summer base flow conditions. Date was an influential random variable at both the microhabitat and reach scale. The best reach models show that surveys performed at later dates exhibited a net positive effect on salmonid catch-per-minute suggesting salmonid relative abundance increased in reaches approaching late summer. Salmonid reach relative abundance may have been higher in reaches during late summer days as an instinctual response to seasonal stream temperature patterns. As stream water temperatures generally trend towards air temperatures in a downstream direction, stream-dwelling salmonids may exhibit upstream movement behaviours as way of avoiding temperature stress even during cool summers.

Lake Superior tributary streams serve as a critical habitat for multiple native and introduced species of salmonid. Multiple salmonid species spawn in these tributary streams and juvenile migrants depend on natal streams to forage and eventually grow enough to migrate into Lake Superior. For species like the Brook Trout, tributary streams are especially important because a portion of their population consists of stream resident ecotypes which spend their entire lives in their natal streams. As the presence of cool water habitats have been shown to influence salmonid abundance and distribution within a stream, sustainable land use practices that maintain the thermal integrity of streams and allow for unimpeded fish movements should allow Lake Superior and its tributary streams to continue supporting healthy salmonid populations.

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