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The Mixed Source Chinook Salmon Fishery in Lake Huron: A Comparison of Spawning and Foraging Habitat Use by Naturalized and Hatchery Fish

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A thesis submitted in partial fulfillment of the requirements for the Doctor of Philosophy degree in Biology

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Abstract

Chinook salmon (*Oncorhynchus tshawytscha*) were introduced into the Great Lakes to restore top-down control of the food web and create new recreational fisheries. Soon after introduction, naturalized spawning populations became established, and with continued stocking of hatchery fish, created a mixed source fishery. My research provides new ecological information about the contributions of naturalized fish to the mixed source Chinook salmon fishery in Lake Huron. I examined spawning and foraging habitat use by naturalized and hatchery Chinook salmon using multiple methods to identify sources of individual fish (external tags, hatchery fin clips, and otolith microchemistry). In the Sydenham River, Ontario, one of the earliest sites of documented natural reproduction, hatchery fish composed >50% of spawning fish in 2010 and 2011. Hatchery and naturalized fish arrived and spawned throughout the river in similar patterns despite evidence of hatchery females directly homing to their stocking site. Increased pre-spawning movement by smaller and later arriving females was evidence that similar habitat use may have resulted from despotic behaviour in the limited amount of accessible habitat (≈ 6 km). Thus, hatchery and naturalized fish showed some differences in behaviour but showed no evidence of reproductive isolation in space or time. I used otolith microchemistry and hatchery fin clips to assigning natal source to Chinook salmon captured in the 2008 and 2010 fisheries to examine in-lake stock composition. In the lake, naturalized fish comprised 66% of fish sampled and the majority of these naturalized fish originated from rivers flowing into Georgian Bay (55%) and northern Lake Huron (35%) while most hatchery fish originated from Michigan hatcheries (67%). Furthermore, there was evidence of incomplete mixing and extensive interbasin movement. Georgian Bay rivers contributed fish lake wide, Michigan hatcheries were dominant contributions in Northern Main Basin, and contributions of fish from central and southern Lake Huron rivers were limited. My thesis provides the first individual based examination of habitat use by naturalized and hatchery Chinook salmon in the Great Lakes, providing basic but crucial information needed by researchers and managers for understanding population dynamics and for sustainably managing the lake ecosystem.

Keywords

Great Lakes, Pacific salmon, introduced species, hatchery effects, recreational fisheries, otolith microchemistry, mixed stock fishery, fish migrations, spatial and temporal distributions, tagging, pre-spawning movements, stream ecology.

Co-Authorship Statement

Chapter 2: Habitat use and arrival timing of hatchery and naturalized Chinook salmon (*Oncorhynchus tshawytscha*) spawning in a Great Lakes tributary.

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- *S.A.C. Marklevitz* planned, coordinated and implemented the study, collected and analyzed the data, wrote and is corresponding author on the manuscript.

Chapter 4: Otolith microchemistry reveals spatio-temporal heterogeneity of natal sources and inter-basin migrations of Chinook salmon in Lake Huron

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- *S.A.C. Marklevitz* planned, coordinated and implemented the study, conducted sample analysis and statistical analysis, wrote and is corresponding author on the manuscript.

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List of Abbreviations, Symbols and Nomenclature

AIC - Akaike Information Criterion

age- X - age of fish X ; age-0 (juveniles), age-1 (one year olds), age-2+ (>2 years old)

ANOVA - Analysis of variance

Br - barium

C - carbon

Ca - calcium

CFIP - Community Fisheries Involvement Program

CH_c - Central Lake Huron capture location

CH_n - Central Lake Huron natal source

C_{ijk} - observed number of fish caught from origin i and sex j on day k

df - degrees of freedom

$F_{n,d}$ - F statistic with numerator (n) and denominator (d) degrees of freedom

FCO - fish community objects (of the Great Lakes Fishery Commission)

Fe - iron

f_k - total length of trap deployment (hours) on day k

GB-1-4 - Georgian Bay Statistical fishery management units

GLFC - Great Lakes Fishery Commission

H - hatchery-reared fish

HMLM - Hierarchical mixed linear model

K - potassium

K-S test - Kolmogorov–Smirnov tests

LA-ICP-MS - laser-ablation inductively-couple-mass-spectrometer (ICP-MS)

LDFA - linear discriminant function analysis

MANOVA - Multivariate analysis of variance

MH 1-6 - Michigan-Huron Statistical fishery management units

$\max\{p_{\text{assign}}\}$ - maximum posterior probabilities of assignment

Mg - magnesium

Mn - manganese

N - naturalized fish

N - estimated populations size

N_{ijk} - estimated number of fish (N) from rearing-origin i of sex j on day k

n - samples size

NC1-3 - North Channel Statistical fishery management units

NH_c - Northern Lake Huron capture location

NH_n - Northern Lake Huron natal source

NIST - National Institute of Standards and Technology

O - oxygen

OH1-5 - Ontario-Huron Statistical fishery management units

OMNRF - Ontario Ministry of Natural Resources and Forestry

p - p-value

p_{assign} - posterior probabilities of assignment

PIT - passive integrated transponders

q - catchability coefficient

r^2 - R-squared

Rb - rubidium

SCAA - Statistical-Catch-At-Age

SE - standard error

SH_c - Southern Lake Huron capture location

SH_n - Southern Lake Huron natal source

Sn - tin

Sr - strontium

$^{87}\text{Sr}/^{86}\text{Sr}$ - Strontium 87 to Strontium 86 ratio

T_{df} - T-test with degrees of freedom (df)

Wald X^2 - *Wald Chi square test*

Wilks λ - Wilks Lambda

X^2 - Chi-square test

Z_{n, d} - Z statistic for HMLM with numerator and dominator degrees of freedom

Zn - Zinc

1 General Introduction

A central goal of contemporary ecology is understanding and predicting the spatio-temporal dynamics of populations including habitat use (Sutherland et al. 2013). How individual-level processes interact with heritable traits and environmental conditions to result in the spatio-temporal patterns observed in nature remains poorly understood. The habitat occupied by individuals and distribution of populations through space and time forms the basis of their ecological niche with implications on foraging, competition (intra- and inter-specific), reproduction, predation, parasitism and diseases. Many of these ecological characteristics directly affect individual fitness and subsequently have evolutionary consequences including phenotypic and genotypic trait divergence or even speciation. For many species, spatial and temporal use of habitats also determine the vulnerability of populations to anthropogenic activities such as fisheries. In species managed (exploited) for human use, understanding and predicting the spatio-temporal dynamics of populations become even more important as it helps define ecological relevant units, which are crucial for sustainably managing and limiting risks of overexploiting the species or individual populations.

Virtually all fisheries in the world are composed of a mixture of fish from different populations originating from different habitats, making them mixed source or mixed stock fisheries (Walters and Martell, 2004). The United Nations generally defines a “fishery” as the activities leading to harvesting (i.e., capture) of fish (including shellfish) which result from wild capture or artificial raising (i.e. aquaculture/fish farming) (FAO, 2014). As a unit, a fishery is defined by the targeted species, area of water fished, fishing methods, people involved, and purpose of activity (e.g., commercial, recreational, or subsistence) (Fletcher et al. 2002). A fish “stock” is a functional unit forming the bases of fisheries management and assessment, and has been used to refer to a species as a whole, or units within a species such as race, population or sub-population (Brooke, 1981; Hawkins et al. 2016). Generally, a stock has been defined as a self-sustaining population or group of ecologically connected populations within a species that occupy a definable area (Brooke, 1981; Hawkins et al. 2016). More specifically, a stock has previously been defined as a genetic unit (genotype) identified through analysis of genetic or phenotypic (physical

traits) markers without variation over time (Brooke, 1999). Recent advancements in stock identification methods have identified unique phenotypic, migration and dispersal patterns within genetic units, suggesting the importance of ecological and not simply genetic connectivity for defining a stock (Hawkins et al. 2016). Genetic connectivity (or panmixia) can occur when only a few individuals disperse among populations or stocks to exchange genetic material within a generation but true ecological connectivity requires significant numbers of dispersing individuals in most years. For the purpose of this thesis, I will use the Hilborn and Walters (1992) definition of a fish “stock” being an arbitrary collection of fish populations that are self-reproducing and show similar growth, migration and dispersal patterns (Hilborn and Walters, 1992). Knowing the contribution from populations and understanding how individuals from different populations interact with each other and move through the ecosystem over time is fundamental to defining ecologically relevant stocks and sustainably managing mixed source fisheries.

Information about stock structure can be qualitatively used to guide scientific and assessment study design and direct management actions. For example, to conserve threatened or overexploited populations, management agencies could implement protected areas (i.e., fish sanctuaries) in crucial habitats where fish aggregate and closures of fisheries at appropriate times along migratory routes. Origins, movements and interactions of populations may also be quantitatively incorporated into fisheries models to estimate fish abundances over time, and bioenergetics or food web models to predict the effects of predation and/or competition (Walters and Martell, 2004).

In the absence of information, fisheries scientists and managers must make simplifying assumptions. Commonly, in the absence of information, a fishery is treated as a “simple dynamic pool” in which changes in abundances are due to recruitment, natural mortality and fishery mortality with no consideration of fish migratory behaviors including immigration or emigration. Recruitment is defined as the process of fish entering an exploitable fish stock and becoming catchable by a fishery, usually resulting from fish growing to a catchable size (FAO, 2014). Natural mortality is defined as the deaths of fish and removal from the fishery not caused by fishing (i.e. fishing mortality) usually resulting from age, predation, diseases and parasitism (FAO, 2014). Fishing mortality is death caused by the fishery or the fish harvested (i.e. caught and kept).

Migration is defined as the systematic movement of individuals from a stock through space and time (e.g. migration from natal areas to feeding/foraging grounds) (FAO, 2014). In terms of fisheries, immigration or emigration refers to fish moving into or out of a fishery through migration. Actual changes observed in fisheries may be more rapid and complex than predicted based on the assumptions of a simple dynamic pool. One such example is the introduced Chinook salmon (*Oncorhynchus tshawytscha*) fisheries in Lake Huron and the other Laurentian Great Lakes.

When originally introduced, it was assumed that indefinite stocking would be required to sustain Chinook salmon fisheries in the Great Lakes (Crawford, 2001). Stocking is defined as the intentional release of artificially reared (hatchery-reared) fish into rivers and lakes. Management plans were made that assumed a simple dynamic pool with lake wide abundances directly related to stocking rates (numbers of fish stocked annually) (Crawford, 2001; Claramunt et al. 2013). However, by the 1990s, reproduction by feral or naturalized populations had become a significant component of these fisheries (Peck et al. 1999; Connerton et al. 2009; Johnson et al. 2010; Tsehaye et al. 2014). Invasion ecology literature has used several different words to describe the transport, introduction (intentional or not) and establishment of species such as Chinook salmon in the Great Lakes including invasive, feral, introduced, non-native, non-indigenous and naturalized (Lockwood et al. 2007). Gross (1998) used the term “exotic species” to describe the Atlantic salmon, *Salmo salar*, fisheries in non-native ranged resulting from intentional release. This classification however does not differentiate between hatchery-reared and stream-reared individuals as such are present with Chinook Salmon in the Great Lakes. For the purpose of this thesis, hatchery-reared and stocked fish will be referred to as hatchery fish. Natural stream-reared fish commonly referred to as “wild” in Great Lakes literature will be referred to as “naturalized” because this captures the true nature of their life history (i.e. non-native but born and raised in the natural environment). The term “wild” will be reserved for referring to naturally reared individuals from native populations.

A lack of knowledge about naturalized fish (including their rivers of origins) resulted in the assumption that naturalized fish were similar to hatchery fish in terms of habitat use, survival, natural mortality, catchability, and recruitment, and the assumption

that fisheries were completely mixed within the lakes regardless of their origins (Adlerstein et al. 2007; 2008; Brenden et al. 2012; Tsehaye et al. 2014). Catchability is a term for the fraction of a fish stock caught by a unit of fishing effort (Ricker, 1975), which may vary as fish grow and recruit to the fishery and could be influenced by migration. The objective of my Ph.D. research was to test these assumptions, by testing for differences in the use of spawning and foraging habitat between naturalized and hatchery fish and examining the contributions of naturalized fish to the Lake Huron fishery.

1.1 Habitat use by Pacific salmonids

Pacific salmonids (*Oncorhynchus* spp.), such as Chinook salmon, show diverse habitat use throughout their life history (Quinn, 2005). These mostly anadromous (return from ocean to spawn in rivers) or potamodromous (return from lakes to spawn in rivers) fish can migrate hundreds to thousands of kilometres down natal rivers into oceanic or limnetic environments to forage (Healy, 1991; Quinn, 2005). Prior to reproducing, adult salmon migrate back from open water foraging areas to their natal sites in rivers; a trait referred to as philopatry or natal homing.

In rivers, salmon navigate back to their natal sites by following olfactory cues sequentially imprinted during downstream migration as juveniles (Horrall, 1981; Dittman and Quinn, 1996). While there is spatial accuracy and precision of homing, the timing of fish returning to natal rivers can also be synchronous (precise) within populations and the onset of spawning (spawning timing) has been shown to be highly heritable trait (Quinn et al. 2000, 2002).

Natal philopatry and synchrony operate at broad scales (e.g., > 1 km, > weeks), enabling fish to arrive at approximately the right location at approximately the right time. At finer spatial scales (e.g., < 1 km, < weeks), environmental conditions, phenotypic traits, behavioural traits and life history experiences influence habitat use. For example, there are high correlations between interannual differences in the timing of upstream migrations and environmental conditions including sea surface and river temperatures and river flow rates (Quinn and Adam, 1996; Hodgson and Quinn, 2002; Hodgson et al. 2006). Salmon may also show sexual dimorphism in spatial and temporal habitat use,

with males commonly arriving sooner and appearing to have less precise natal homing than females (Morbey, 2000; Neville et al. 2006). In both sexes, phenotypic traits (i.e., body size and secondary sexual traits) and phenology have important roles in individual spawning site selection, with larger and earlier arriving individuals occupying the most favourable locations (Foote, 1990; Quinn and Foote, 1994; Hendry et al. 2001; Schroder et al. 2008; Adkison et al. 2014). Previous studies examining hatchery rearing and release practices demonstrate that early life history experiences such as location and timing of release can also influence where and when fish return and rates of natal homing (Unwin and Quinn, 1993; Pascual et al. 1995; Quinn et al. 2002; Dittman et al. 2010).

In open water, it is not fully understood how individuals are able to navigate over such great distances (100s - 1000s km), with the accuracy and precision required to return to natal rivers. In marine animals such as sea turtles (i.e., *Cheloniidae* and *Dermochelyidae* spp.), marine mammals (i.e., cetaceans and pinnipeds) and fish, several mechanisms have been hypothesized. These include visual (celestial), hydrodynamics (currents), and olfactory cues; internal compasses with simple cognitive maps and the use of geomagnetic fields (Lohmann et al. 2008). Recent evidence suggests salmon use imprinted geomagnetic cues and the Earth's geomagnetic field for open water navigation (Bracis and Anderson, 2013; Putnam et al. 2013). Other evidence suggests salmon use photoperiod as a temporal cue to time migrations from foraging areas so they arrive in spawning rivers when environmental conditions (i.e., river temperature and flow) are favourable for reproductive success and offspring survival (O'Malley et al. 2007, 2010).

Decades of tagging studies on Pacific salmonids have demonstrated diversity in the open water habitat use among species and populations (Quinn, 2005). Many species, including chum (*O. keta*), pink (*O. gorbuscha*), and sockeye (*O. nerka*) salmon, are known to move northwards into offshore waters within the first year of ocean residency (Quinn, 2005; Myer et al. 2007). In comparison, Chinook salmon generally have a longer northward migration (> 1yr) and tend to remain in coastal waters (Quinn, 2005; Weitkamp, 2010).

Chinook salmon have two life history types or races, "ocean-type" and "stream-type" with distinct patterns of habitat use (Healy, 1991; Quinn, 2005). Ocean-type populations typically enter rivers shortly (days to weeks) before spawning and then spawn

in late summer or fall with offspring emigrating from natal rivers the following spring. Stream-type populations typically enter rivers months before spawning and then spawn in spring and summer with offspring spending a year or more in freshwater before emigrating into the ocean. Once in open water, ocean-type fish tend to remain in inlets and coastal waters (< 80 km from the coast), while stream-type fish more commonly move into offshore waters (> 80 km from the coast) (Healy, 1983, 1991).

The geographical location of populations (i.e., natal river) highly influences open water habitat use. The largest study to-date examined the spatial capture patterns from 632,257 Chinook salmon in the North Pacific between 1979 and 2005 (Weitkamp, 2010). This study found evidence of annually consistent, region-specific distributions. Findings also confirmed previous observations of northward migration by populations located north of Cape Blanco (Oregon, USA) and southward migration of populations located south of Cape Blanco (Nicholas and Hankin, 1988; Weitkamp, 2010). Some populations also appeared to display residency behaviours and remained in proximity of natal rivers and hatcheries (Weitkamp, 2010; Chamberlin et al. 2011; Quinn et al. 2011). At finer spatial scales, it appears that local oceanic conditions at the point of entry can also influence the open water habitat use (Chamberlin et al. 2011).

1.2 Hatchery effects

A concern for scientists and managers is that most information about spawning and foraging habitat use by salmonids has been derived from data collected on hatchery fish. For example, only 1.9% of the Chinook salmon in the Weitkamp (2010) study were naturalized fish. Furthermore, many studies on natal homing accuracy and precision are based on returning hatchery fish (e.g., Quinn and Fresh, 1984, Dittman et al. 1996, Dittman et al. 2010; Westley et al. 2013). The assumption of similar habitat use by hatchery and naturalized fish may be inappropriate because artificial selective pressures and carry-over effects of hatchery rearing can alter phenotypic and behavioural traits and result in different habitat use by hatchery fish. “Carry-over effects” are defined in ecology as the effects on an individual’s performance in a given situation resulting from their previous life history or experiences (O’Connor et al. 2014). Supplemental hatchery programs such as those in the Great Lakes attempt to maximize the survival rate of fish

through critical early life history stages while maintaining the genetic and phenotypic diversity of the donor population (Huntingford, 2004). Gametes are collected from naturalized populations, artificially fertilized and incubated in trays with continuous flow of oxygenated water. Once offspring emerge from eggs they are transferred to holding tanks and reared at high densities with similar sized conspecifics. Holding tanks are often simple environments, devoid of natural features such as instream structures, substrates and predators. In hatcheries, fish are supplied with an abundance of high quality pelleted food.

Hatchery rearing can result in altered aggression and boldness (i.e., lower predator avoidance) and reduced hunting abilities in juveniles (Huntingford, 2004; Glover et al. 2004; Sundstroem et al. 2004; Fernoe et al. 1998, Ruzzante, 1994; Pearsons et al. 2007). Hatchery fish may also have reduced growth rates, smaller size at maturity (e.g., Knudsen et al. 2006, 2008; Schroder et al. 2008, Theriault et al. 2010; Weber and Fausch 2004), smaller egg sizes and fecundity (e.g., Knudsen et al. 2008; Jastrebski and Morbey 2009), and lower sperm concentration in their milt (e.g., Poole and Dillane, 1998). Spawning adults may display lower social dominance and inappropriate spawning behaviours (e.g., poor nest construction, nest abandonment, incomplete spawning attempts) (Fleming et al. 1996, 1997; Schroder et al. 2008, 2010, 2012). Artificial selection on arrival and spawning timing during gamete collections may result in hatchery fish that arrive and spawn at times that are different from naturalized fish in the same river (e.g., Quinn et al. 2000, 2002). Carry-over effects of stocking practices (i.e., stocking location and timing) can affect timing of juvenile out-emigration from rivers, open water distributions during foraging, homing rates and spatial distributions of spawning adults (Unwin and Quinn, 1993; Pascual et al. 1995; Dittmann and Quinn, 1996; Daugherty et al. 2003; Hoffnagle et al. 2008; Dittman et al. 2010; Chamberlin et al. 2011).

1.3 Chinook salmon in the Great Lakes

In Lake Huron and the other Great Lakes, fisheries management agencies intentionally introduced and continuously stock Chinook salmon to restore predator-prey balance and augment declining recreational fishing opportunities (Crawford, 2001; Claramunt et al. 2013). Since European settlement, the lakes have seen drastic alterations

to the ichthyofauna and ecosystems (Kocik and Jones, 1999). Colonization of the region by invasive sea lamprey (*Petromyzon marinus*) had especially devastating ecological consequences because these parasitic fish preferentially target large bodied fish species such as lake trout (*Salvelinus namaycush*), burbot (*Lota lota*), lake whitefish (*Coregonus clupeaformis*) and other cisco species (*Coregonus* spp.). By the 1950s, the combination of lamprey parasitism, overfishing, and habitat alteration were implicated in significant declines in the native apex piscivore, lake trout (Hensen, 1999). In the absence of abundant large-bodied piscivores, the ecosystem became dominated by alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) that are invasive, small-bodied forage species (Kocik and Jones, 1999; Claramunt et al. 2013).

Stocking of Chinook salmon began in 1967 with releases into Lakes Michigan and Superior. These stocked fish were the offspring of ocean-type, Green River (Washington, USA) Chinook salmon transported and reared for 5 - 6 months in Michigan State hatcheries (Weeder et al. 2005; Claramunt et al. 2013). Stocking quickly expanded into Lakes Huron (1968), Ontario (1969), and Erie (1970). After 1969, no additional embryo transfers from Washington State were required because returns of mature fish to stocking sites provided local sources of gametes (Suk et al. 2011). By 1977, Chinook salmon were stocked by all US states bordering the Great Lakes (Kocik and Jones, 1999; Claramunt et al. 2013). Stocking in Canada was significantly more restricted. The Ontario Ministry of Natural Resources and Forestry (OMNRF) began stocking into Lake Ontario in 1971 and through the Community Fisheries Involvement Program (CFIP) into Lake Huron and Lake Superior in 1985. CFIP is a unique program because the OMNRF regulates stocking rates while local angling and conservation groups implement stocking programs. Stocking intensified in all Great Lakes until the late 1980s when evidence suggested that many of the lakes were being overstocked (Crawford, 2001). Overstocking refers to stocking more fish into the lakes than can be supported by the abundances of forage species. Stocking rates have gradually declined since that time (Claramunt et al. 2013). In Lake Huron, stocking peaked in 1988 (5 million fish stocked) with reductions in 1990 (4.5 million fish \cdot yr⁻¹), 1999 (3.5 million \cdot yr⁻¹) and through the 2000s to 2009 levels (1.5 million \cdot yr⁻¹) where they have remained (Crawford, 2001; Johnson et al. 2007; Johnson and Gonder, 2013).

Soon after the initial introductions, successful naturalized reproduction of Chinook salmon was observed in tributaries of Lakes Michigan (Rybicki, 1973), Superior (Peck, 1992), Huron (Kerr and Perron, 1986) and Ontario (Smith, 1995). Evidence of shoal spawning Chinook salmon was also discovered on historical lake trout spawning shoals around Manitoulin Island in northern Lake Huron (Powell and Miller, 1990). To date, the most extensive survey has identified 17 naturalized populations in Lake Huron tributaries (Marklevitz et al. 2011). By the mid-1980s, naturalized reproduction contributed > 20% of the fishery in some lakes (Carl, 1982; Peck et al. 1999). During the 1990s and 2000s, the majority (> 50%) of fish in some fisheries came from naturalized populations (Connerton et al. 2009; Johnson et al. 2010; Tsehaye et al. 2014). During the 1990s, annual contributions from naturalized populations to the Lake Huron fishery was estimated at 15% or approximately 790,000 fish annually based on a Statistical-Catch-At-Age (SCAA) model (Bence et al. 2008; Brenden et al. 2012). During the 2000s, annual contributions from naturalized populations grew to an estimated > 80% or >10 million fish annually (Johnson et al. 2010; Brenden et al. 2012).

Chinook salmon have successfully reduced abundances of invasive alewife and rainbow smelt and restored top-down control (i.e. predator controlled forage species abundances) of these invasive species across the Great Lakes region (O’Gorman et al. 2004; Madenjian et al. 2005, 2008; Riley et al. 2008). In fact, their ability to preferentially consume invasive forage species, particularly alewife, has placed and continue to maintain substantial top-down control on these invasive forage species (Jacobs et al. 2013; Tsehaye et al. 2014). The presence of Chinook salmon has also created and supported new fisheries for large, charismatic fish that are highly desired by recreational fishers.

Recreational fisheries in the Great Lakes are worth an estimated \$3 billion annually and Chinook salmon represent 58% of all recreationally harvested fish in Lake Michigan and 58% and 40% of recreational salmonid fisheries in Lakes Huron and Ontario, respectively (Claramunt et al. 2013; Thayer and Loftus, 2013). Commercial fisheries for Chinook salmon are limited to a small First Nation’s fishery in US waters of Lakes Michigan, Huron and Superior but the commercialization of the recreational fishery through charter fishing operators has major economic value. For example, in 2002,

approximately \$10 million was spent by anglers using Michigan charter operators; many of which were likely targeting Chinook salmon in Lake Michigan.

Given the establishment of naturalized populations, their top-down control of invasive forage species and importance as recreational fisheries, Chinook salmon are now part of the Great Lakes ichthyofauna in Lakes Michigan, Huron, Superior, and Ontario (Kocik and Jones, 1999). Their place within fisheries and the ecosystems of these lakes are ingrained in the Great Lakes Fishery Commission's (GLFC) fish community objects (FCOs) (DesJardine et al. 1995; Eshenroder et al. 1995; Horns et al. 2003; Stewart et al. 2013). The GLFC facilitates binational (US and Canada), multi-agency (federal, state, provincial and tribal environmental and natural resources agencies and academic institutions) research, management and consultation with community partners (e.g., non-governmental organisations and community interest groups) in issues pertaining to Great Lakes fisheries (www.glfc.org). The FCOs are developed independently for each lake by the management agencies with jurisdiction within each lake under the Joint Strategic Plan for the Management of Great Lakes Fisheries (GLFC, 2007, Stewart et al 2013). FCOs provide a unified set of objectives and guiding principles for fisheries management.

Historically in the Great Lakes, management of Chinook salmon fisheries has primarily focused on balancing predator with prey abundances through the manipulation of stocking rates (e.g., Stewart et al. 1981; Jones et al. 1992; Dobiesz, 2003; Whelan and Johnson, 2004). This management strategy treated the fisheries within each lake as singular simple dynamic pool and assumed that indefinite stocking would be required to sustain these fisheries and abundances were directly related to stocking rates (Crawford, 2001; Claramunt et al. 2013). These management plans neglected the increasing contribution from naturalized populations. In Lake Huron, the contributions of naturalized fish in addition to stocked fish likely led to a prey-limited situation where predator demand exceeded prey availability (i.e., overstocking) (Roseman and Riley, 2009). Overstocking was largely thought to be the cause of the smaller size and emaciated condition of Chinook salmon observed during the late 1990s and potentially the 2003 collapse of alewife (Johnson et al. 2007; Roseman and Riley, 2009). Modelling appears to support the role of Chinook salmon overstocking in the presence of significant naturalized contributions as a factor for the 2003 alewife collapse and lack of recovery since that time

(He et al. 2015). However, this opinion is not shared by all fisheries researchers and there is some debate about the influence of cold winter temperatures in the alewife collapse (see Dunlop and Riley, 2013; Riley and Dunlop, 2016 and Bence et al. 2016). There are concerns that overstocking in a prey-limited situation may also impede restoration efforts of native lake trout (Roseman and Riley, 2009). While fisheries researchers and managers have long known about the presence of naturalized Chinook salmon, they have lacked basic ecological information including the origins of these fish (e.g., US or Canadian rivers), how different naturalized populations contribute to in-lake fisheries and whether there are differences in habitat use between naturalized populations and hatcheries.

Unlike populations along the west coast of North America, there is no extensive monitoring of salmon populations in the Great Lakes to estimate numbers of returning adults or numbers of juveniles migrating out the rivers. Research and monitoring of naturalized Chinook salmon have been particularly lacking in Great Lakes tributaries. A few studies have identified naturalized populations in some tributaries through the presence or absence of spawning adults and juveniles (e.g., Carl, 1982; Kerr and Perron, 1986; Marklevitz et al. 2011). To date, most research and monitoring of Chinook salmon in Lake Huron and the other Great Lakes has focused on the captures of fish in recreational, in-lake fisheries. Furthermore, most information has been based on or derived from data of recaptured hatchery fish. A pair of studies examined capture patterns of coded wired tagged hatchery fish in Lake Huron and Lake Michigan (Alderstein et al. 2007, 2008). These studies primarily collected salmon in US waters and found extensive seasonal migrations of fish suggesting extensive movement supporting the assumption that the fishery was a singular simple dynamic pool (Alderstein et al. 2007). The best estimates of the amount of recruitment of naturalized fish are derived from the ratios of hatchery to naturalized fish captured in fisheries (e.g., Bence et al 2008; Connerton et al. 2009; Johnson et al. 2010). Johnson et al. 2010 concluded that the significant contribution (> 85%) of naturalized fish throughout Lake Huron was evidence that naturalized populations could sustain the fishery.

Relative contributions of naturalized fish were subsequently used in Statistical-Catch-At-Age (SCAA) models to estimate abundances of hatchery and naturalized Chinook salmon in Lakes Huron and Michigan (e.g., Brenden et al. 2012; Tsehaye et al.

2014). SCAA models consist of a series of age-specific sub-models which use information about age-specific mortality (natural and fishing), vulnerability to the fishery (catchability), weights and fecundity to predict total and age-specific recruitment (to the fishery), catches and abundances in fisheries (Hilborn and Walters, 1992). Models are not unidirectional; for example, information about catches and recruitment can be used to estimate catchability, mortality and abundances.

Brenden et al. (2012) developed a SCAA model to estimate abundances of Chinook salmon in Lake Huron. This model used recruitment rates based on stocking rates for hatchery fish and relative abundance of naturalized to hatchery fish captured in the fishery (e.g., Bence et al. 2008; Johnson et al. 2010). Catch (harvest) and effort data were predominately based on recreational fisheries in Michigan waters, because limited and intermittent monitoring in Ontario waters meant the catch and effort data needed to be indexed to the Michigan fishery to produce annual estimates. This limited monitoring in Ontario waters also meant that age composition and proportion of mature fish were solely derived from the Michigan fishery. Weight-at-age data used to estimate a probability of maturation was also collected from the Michigan fishery and hatchery fish returning to Swan River weir. Similar to many fisheries model this SCAA required numerous assumptions. The first assumption was that the Chinook salmon fishery in the Main Basin of Lake Huron is a simple dynamic pool (single well-mixed stock) with no immigration or emigration. The authors highlighted the potential for violations to this assumption, but suggested results from Adlerstein et al. (2007, 2008), Weeder et al. (2005) finding of a panmictic Lake Michigan population and a lack of information to suggest alternative stock structure or migration patterns provided sufficient rational for this assumption. The second assumption was the equal rate of survival of hatchery and naturalized fish. The authors admit this assumption was likely incorrect and made out of necessity because of a lack of data to suggest otherwise. If survival of naturalized fish is higher than hatchery fish there is a potential that the model underestimates naturalized abundances. While this SCAA is our best and most comprehensive estimate of Chinook salmon abundances in Lake Huron, the lack of information about naturalized populations and stock structure of the fishery presents a large uncertainty with potentially significant effects on model estimates including naturalized abundances.

1.4 Thesis structure

The objective of my Ph.D. research was to provide basic ecological information about the habitat use of naturalized and hatchery Chinook salmon in Lake Huron in order to address critical knowledge gaps required to properly understand and model population dynamics and for sustainable management of the fishery. My research had three goals: 1) identify origins of naturalized fish; 2) identify how naturalized and hatchery fish contribute to a spawning population and to in-lake fishery; and 3) test for differences in habitat use during spawning and foraging between hatchery and naturalized fish. Using various techniques (i.e., tagging, hatchery marking and otolith microchemistry) to identify origins of fish, I used an individual level approach to examine spatial and temporal use of habitat in a spawning river and the lake.

My research was composed of two distinct projects: 1) spawning habitat use; and 2) foraging habitat use. Project One (Chapter 2) examined the spawning habitat use of naturalized and hatchery Chinook salmon in the Sydenham River (Owen Sound, Ontario). This river was one of the first tributaries of Lake Huron with documented naturalized reproduction (Kerr and Perron, 1986). It also has a CFIP hatchery operated by the Sydenham Sportsmen's Association. This hatchery program has annually released fish into the river to supplement the recreational fishery since 1985. Starting my examination of habitat use by naturalized and hatchery fish in a spawning river provided two advantages. First, by tagging and tracking individuals it afforded the opportunity to make detailed observations in the natural environment over time. I was therefore able to observe behaviours (pre-spawning movements) leading up to final spawning site selection in addition to the spawning habitat use by adults. I found no difference in habitat use by hatchery and naturalized Chinook salmon. The timing of arrival to the river was similar within sexes and between rearing origins. However, the extent of pre-spawning movement up and down the river by females increased with arrival date, decreased with fish length and was greatest for naturalized fish. Starting my research in a river and making detailed observations also allowed me to test for the persistence of hatchery rearing effects through the adult life history phase. For example, the observed differences in male phenotypic traits (i.e., length, weight, hump height) were evidence of persistent hatchery effects that may have resulted from selection of body size during gamete

collection, alterations in life history (i.e. age at maturation) or differences in open water habitat use during foraging (Kinnison et al. 2003; McLean et al. 2005; Knudsen et al. 2006; Wells et al. 2006, 2008)

Project Two (Chapters 3 and 4) examined the foraging habitat used by naturalized and hatchery Chinook salmon from different regions in Lake Huron. A major limitation to understanding habitat use and the ecology of any fish species in open water is the ability to reliably identify the origins of fish. Logistical and financial limitations can impede the ability to implement mass marking studies at spatial and temporal scales relevant to fisheries, especially when tagging naturalized populations. Another approach is to use natural markers of natal sources. In the Great Lakes, genetic analysis of Chinook salmon populations has demonstrated typical genetic markers of population structure such as allozymes and microsatellites to be minimally useful. Weeder et al. 2005 found no differences in 18 allozymes markers among Lake Michigan populations suggesting random breeding among populations (or panmixia). In Lake Huron, Suk et al (2011) found some differences in nine microsatellite markers but only in three populations (Maitland River, Root River and Nunn's Creek); the remaining populations were similar. Otolith microchemistry provides an alternative approach. Otoliths or the earbones of fish continuously grow incorporating elemental impurities into the calcium carbonate structure at concentrations reflective of the habitat occupied by a fish (Campana, 1999). Using juvenile salmon collected from known natal sources, I previously demonstrated the potential use of otolith microchemistry as a natural marker for identifying natal sources of Chinook salmon in Lake Huron (Marklevitz et al. 2011). By analysing the juvenile sections in adult otoliths and applying the predictive model from Marklevitz et al. (2011), I planned to assign natal origins of adults captured in the lake. However, questions remained about the ability to accurately analyse the juvenile sections in adult otoliths, and the literature did not provide a consistent answer.

In the literature, studies typically used one of four methods to locate and analyse juvenile otolith sections: A) whole juvenile otoliths; B) sections a standard distance from the core; C) sections at the otolith edge; or D) sections related to a life history event recorded in the microchemistry. In Chapter 3, I quantitatively compared microchemical concentrations and the subsequent performance of the four methods using a common

dataset. Method performance was assessed three ways: 1) site-specific assignments of individual fish; 2) frequency (%) at which method could be applied to the common dataset; and 3) temporal stability of microchemical concentrations. Microchemical concentrations differed among methods. Site-specific assignments were similar among methods with 94% - 100% of fish assigned to sites in geographical proximity of the correct site (including the correct site). Method applicability differed, ranging from 54% to 98%. No method produced temporally stable microchemical concentrations. These findings indicated that method choice was less important than analysis of consistent otolith sections, highlighting the need to take the three dimensional structure of otoliths into consideration for microchemical analysis. Temporal variability in microchemical signals must also be considered and addressed during study design.

In Chapter 4, I used otolith microchemistry (multi-element concentrations and $^{87}\text{Sr}/^{86}\text{Sr}$ isotopic ratios) and hatchery markings (coded wire tags, oxytetracycline mark, and fin clips) to identify natal sources of individual Chinook salmon collected in the 2008 and 2010 recreational fishery in Lake Huron. Findings suggested that > 90% of all fish in the recreational fishery originate from rivers and hatcheries in Southern Georgian Bay (46%) and Northern Lake Huron (46%). The majority of naturalized fish appear to originate from rivers in Southern Georgian Bay (55%) and Northern Lake Huron (35%), whereas the majority (67%) of hatchery fish appear to originate from Michigan hatcheries. Analysis of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios suggests that < 1% of the fish originated from Canadian Shield rivers east of the St. Marys River. Findings also demonstrated extensive spatial and temporal variability in sample composition, providing the first direct evidence of incomplete mixing of naturalized and hatchery populations in the fishery. By testing for differences in regional composition throughout the lake over time, I produced the first explicit test and falsification of the completely mixed (or mixed stock) assumption commonly used by fisheries management and modelers in the Great Lakes (Adlerstein et al. 2007, 2008; Brenden et al. 2012; Tsehaye et al. 2014).

The intentional introduction, establishment of naturalized populations, and continued stocking of Chinook salmon into the Great Lakes provided an excellent natural experiment and a model system in which we can study sustainable management of a purposely introduced and stocked non-native species. In my final chapter (Chapter 5), I

examined my findings in the context of sustainable fisheries management. I explained the GLFC FCOs for Chinook salmon and the conflicting views of the importance of this non-native species in the Great Lakes. My findings of spawning and foraging habitat use were related to concerns about the sustainability of Chinook salmon in the Great Lakes and fisheries in general. I highlighted the potential of the Chinook salmon in the Great Lakes to be a natural experiment for examining local adaptation and evolution in salmonids, effects of prolonged and intensive stocking programs and broad scale ecosystem manipulation. Furthermore, because I found major violation in the assumptions used by current fisheries management and in SCAA models (i.e., migration and incomplete mixing), I outlined how these assumptions may lead to underestimation of recruitment of naturalized fish and could compromise the sustainability of the fishery. Finally, I presented four recommendations emanating from my research for future research directions to ensure the sustainable management of the Chinook salmon fisheries in the Great Lakes.

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2 Habitat use and arrival timing of hatchery and naturalized Chinook salmon (*Oncorhynchus tshawytscha*) spawning in a Great Lakes tributary

2.1 Introduction

In the Laurentian Great Lakes, large-scale stocking programs to intentionally introduce and maintain Chinook salmon *Oncorhynchus tshawytscha* fisheries represent one of the world's largest ecosystem manipulations (Kocik and Jones, 1999; Crawford, 2001; Claramunt et al. 2013). In addition to providing socioeconomic benefits, intentional introductions can provide useful information about how hatchery supplementation might affect the process of naturalization or the recovery of wild stocks. In the case of Chinook salmon, successful natural reproduction by naturalized populations was documented in Lake Michigan tributaries soon after the initial introductions (Rybicki, 1973), with subsequent discoveries in Lakes Huron (Kerr and Perron, 1986), Superior (Peck, 1992) and Ontario (Smith, 1995). Since the early 2000s, fisheries in Lakes Huron, Michigan, and Ontario have become partially or predominately sustained by naturalized populations but stocking has continued (Connerton et al. 2009; Johnson et al. 2010; Claramunt et al. 2013; Tsehaye et al. 2014). As a result, characterizing the ecological differences between hatchery and naturalized Chinook salmon is becoming an important objective for informing the sustainable management of this species (Kern et al. 2016).

In hatchery supplementation programs, an important issue is whether hatchery fish are reproductively isolated from their wild or naturalized conspecifics, because this can impact program outcomes. Indeed, many studies of salmonids in their native range have found differences in spatial habitat use and the timing of migration and spawning between hatchery and wild fish, even within the same river (e.g., Mackey et al. 2001; Quinn et al. 2002, 2006 Knudsen et al. 2006, 2008; Hoffnagle et al. 2008; Schroder et al. 2008, 2010; Dittman et al. 2010). In the Great Lakes, Kerns et al. (2016) hypothesized that different selective forces between hatchery and naturalized Chinook salmon populations could lead to evolutionary divergence in history traits (fecundity, egg size, timing of spawning and

size at maturity). However, information is lacking on the degree of reproductive isolation between hatchery and naturalized fish in hatchery supplemented populations.

In hatchery supplemented populations, reproductive isolation could arise in two ways. First, hatchery release practices can affect where hatchery-reared fish spawn. According to a behavioral model proposed by Johnsen (1982) with significant modification by Quinn (2005), wild salmon home back to natal sites by performing lateral upstream movements following olfactory cues that were sequentially imprinted as juveniles (Dittman and Quinn, 1996; Quinn, 2005). When adults lose contact with imprinted cues during upstream migration, they backtrack downstream until cues are re-acquired (see fig 5-3 in Quinn, 2005). These behaviors repeat in a trial-and-error fashion as fish search for natal sites. Hereafter, this will be referred to as the Johnsen-Quinn (2005) model. These behaviours appear to result in females precisely homing to within one kilometre of natal sites while some males may disperse (or stray) greater than 40 km from natal sites (Neville et al. 2006). Hatchery fish, which lack incubation-emergence sites, commonly home to their stocking site or the vicinity of their natal hatchery (Garcia et al. 2004; Quinn et al. 2006; Dittman et al. 2010). Timing and location of stocking can influence the imprinting sequence with potential impacts on homing rates of hatchery adults (Unwin and Quinn, 1993; Pascual et al. 1995; Dittmann and Quinn, 1996). For example, homing to stocking sites is highest when hatchery fish are stocked prior to the parr-smolt transformation at times similar to downstream migrations of wild juveniles and when the hatchery and stocking location are in proximity. Hatchery fish will accurately home when properly imprinted to stocking sites, even when introduced to novel environments such as the Great Lakes (Horrall, 1981; Quinn and Fresh, 1984; Dittman et al. 2010; Nack et al. 2011).

Reproductive isolation-by-distance may be further maintained as natal homing yields to individual spawning site selection because different phenotypic (e.g., smaller and younger age at maturity) and behavioral traits (e.g., territoriality) of hatchery-reared fish can affect social dominance and individual site selection (Knudsen et al. 2006, 2008; Schroder et al. 2008, 2010, 2012). When selecting a spawning site, individual salmon use sex-specific environmental and social cues, highly influenced by body size, arrival timing and densities of spawning salmon (Hendry et al. 2001; Schroder et al. 2008; Adkison et

al. 2014). Females search for locations with favorable environmental conditions that appear to be population-specific, while males search for locations affording mating opportunities with females (Foote, 1990; Healey, 1991; Quinn and Foote, 1994; Hendry et al. 2001; Morbey and Ydenberg, 2003; Quinn, 2005). Favorable locations for either sex are highly determinant on levels of intrasexual competition. Through despotic or territorial behaviors, larger and earlier settling fish generally have the competitive advantage and become socially dominant (Foote, 1990; Quinn and Foote, 1994; Hendry et al. 2001; Morbey, 2002; Rich et al. 2006; Berejikian et al. 2010). As a result of individual site selection, spawning salmon are commonly clustered around presumably favorable habitat with the less socially dominant (i.e. smaller and later arriving) individuals occupying less favorable locations at the periphery (Hendry et al. 2001; Schroder et al. 2008; Adkison et al. 2014).

Second, the timing of gamete collections can impose artificial selection on arrival and spawning timing (Quinn et al. 2002; McLean et al. 2005). Spawning times are heritable traits that increase the likelihood that wild fish encounter mating opportunities and favorable conditions for spawning, egg incubation, and offspring development (Quinn et al. 2000, 2002; Quinn 2005). Research on introduced Chinook salmon populations in New Zealand demonstrated that arrival and spawning timing diverged in fewer than 30 generations, likely in response to differing environmental conditions (Quinn et al. 2000). Quinn et al. (2000) concluded divergence of arrival and spawning timing occurs during the initial stages of adaptation to novel selective pressures and could feedback to strengthen reproductive isolation. However, the direction of this divergence appears to be situation specific, with hatchery fish sometimes arriving or spawning sooner, while other times later than wild relatives (e.g., Mackey et al. 2001; Knudsen et al. 2006; Hoffnagle et al. 2008). Quinn et al. (2002) demonstrated very fast artificial selection on spawning times with differences between two Chinook salmon hatchery populations evident in less than ten years.

The objective of this study was to compare the pre-spawning movement, habitat use and timing (arrival, settling, and reproductive life span) between hatchery and naturalized Chinook salmon spawning in the Sydenham River (Owen Sound, Ontario: 44° 34.055'N, 80° 56.647'W), to evaluate the potential for reproductive isolation between rearing-

origins within a Great Lakes tributary. I hypothesized that hatchery fish might display different patterns of habitat use than naturalized fish owing primarily to non-heritable effects (e.g., imprinting) of hatchery practices. To test this hypothesis, I individually tagged fish and followed them from arrival in the river until death. Given releases of hatchery fish in proximity (< 1.4 km) to the hatchery, we expected that hatchery fish to show accurate homing to the stocking site. Following the Johnsen-Quinn (2005) model, I expected hatchery fish to display limited pre-spawning movement upstream of the stocking site. I also expected pre-spawning movement to be sex specific, given that females show greater homing precision and less extensive pre-spawning movements than males (Neville et al. 2006; Anderson et al. 2007). The limited movement past the stocking site should also increase the likelihood of hatchery fish spawning near the stocking site. Differences in pre-spawning movement, habitat use and timing between rearing-origins would provide mechanisms for reproductive isolation and the potential for within-river divergence of hatchery and naturalized fish.

2.2 Methods

2.2.1 Study site

The Sydenham River was one of the first rivers in the Lake Huron watershed in which natural reproduction was documented, and thus a good site to test for the presence of reproductive isolation (Kerr and Perron, 1986; Kerr, 1987). Early colonizers of the river likely originated as straying (i.e., non-homing) hatchery fish, released by the State of Michigan hatcheries (Suk et al. 2011). The river has 6 km of habitat accessible to spawning potamodromous fish species including Chinook salmon (Figure 2.1). All river distances are measured from the 10th Ave. E. bridge (Owen Sound, Ontario) located at the river mouth. At river km-1 is the Mill Dam with a pool and weir fishway enabling fish to ascend 3 m, bypassing the dam structure (Kerr, 2010). At the top of the fishway is a fish-trap which can hold fish in a large steel mesh basket (2 m × 2 m × 1.5 m). Some Chinook salmon were observed spawning in pool and riffle habitat from river km-0.8 to the base of the dam. Between river km-1 to km-3 is the flooded reservoir created by the dam with a shoreline composed primarily of private residential properties. Pool and riffle habitat begins again at river km-3 and persists to the cascades of Inglis Falls (river km-6), an

impassable waterfall preventing further upstream migration. The river flows through a public park from river km-3 to km-3.7. River km-3.7 to km-6 consists of rocky, forested shorelines with some areas of steep cliffs.

In addition to the natural river channel, there are two semi-natural spawning channels with downstream effluences at river km-4.5 and river km-5.0. These channels and a section of the main river between river km-3 to km-3.7 are specifically maintained through the addition of gravel substrate and the creation of pools and riffles as spawning habitat for non-native salmonids, including Chinook salmon, steelhead (Rainbow) trout *Oncorhynchus mykiss*, and brown trout *Salmo trutta*. Combined, the main river and semi-natural spawning channels contain approximately 3.5 km of habitat upstream of the Mill Dam for Chinook salmon spawning.

While the Sydenham River is small (6 km) compared to rivers in the native range of Chinook salmon (e.g., Snake River [1700 km], Imnaha River [118 km] and Yakima River [344 km]), it may be representative of many potential spawning rivers in Lake Huron and the other Great Lakes. In stream barriers including dams, culverts, and waterfalls, limit access to much of the coldwater stream habitat. For example, in the State of Michigan less than 53 km of the 1836 km of coldwater riverine habitat is accessible to migrating salmon from Lake Huron (Gebhardt et al. 1999).

In 1984-85, the Sydenham Sportsmen Association under the Community Fisheries Involvement Program (CFIP) started a hatchery program to supplement the local recreational fishery (Crawford, 2001; Kerr, 1987, 2006). Annual gamete collections for the hatchery occur over short time periods (usually 1 - 4 days) in late September/early October (Denis Wiseman, Sydenham Sportsmen Association hatchery manager, pers. comm.). Fish are captured at the Mill Dam in the fish-trap, directly from the fish ladder, and in an adjacent spillway with a purpose built collection channel. Gametes for the hatchery program are only collected from ovulated females and males able to express milt (seminal fluid) with no intentional selection during collections or gamete pairings based on rearing-origin (hatchery or naturalized) or phenotypic traits (e.g., size). Gametes are then transferred to the hatchery located on Weavers Creek, a small tributary of the Sydenham River.

The hatchery on Weavers Creek is located approximately 1400 m upstream from the effluence into the main river at river km-3.2 (Figure 2.1). Movement of adult Chinook salmon into Weavers Creek is prevented by an exclusion barrier near the effluence into the main river. Each spring juvenile (age 0) hatchery fish are adipose fin clipped for identification and released immediately downstream of the hatchery-stream effluence at river km-2.9, which is downstream of the artificial spawning channels, between May – June (Denis Wiseman, Sydenham Sportsmen Association hatchery manager, pers. comm.); hereafter this site will be referred to as the stocking site. Hatchery and naturalized Chinook salmon return to spawn in the Sydenham River from September to mid-October after spending 2 - 4 yr foraging in Lake Huron (Kocik and Jones, 1999; Marklevitz et al. 2016).

Two other CFIP groups also annually collect gametes from Chinook salmon returning to spawn in the Sydenham River at the Mill Dam. Beyond interrupting my sampling efforts, the impacts of these other CFIP groups on my study are expected to be minimal because gametes are exported to CFIP hatcheries in Point Edward, Ontario (42° 59.982'N, 82° 25.165'W) and Port Elgin, Ontario (44° 26.493'N, 82° 24.001'W) with fish released to locations in proximity of their hatcheries.

2.2.2 Fish tagging

Chinook salmon were intercepted using the fish-trap as they passed through the Mill Dam fishway. The fish-trap was operated daily from 12 September to 15 October, 2010 and 8 September to 19 October, 2011. Field observations suggest these time periods covered the entire period of arrivals. Prior to the start of sampling, no fish were observed in the river and undisturbed fine sediments were present on stream substrate when commencing trap operation. The fine sediments quickly disappeared after the first recorded arrivals of Chinook salmon. Fish trap operation ceased after a period of 4 - 7 days with no new arrivals with fine sediments present on river substrates within a month of the last recorded arrival.

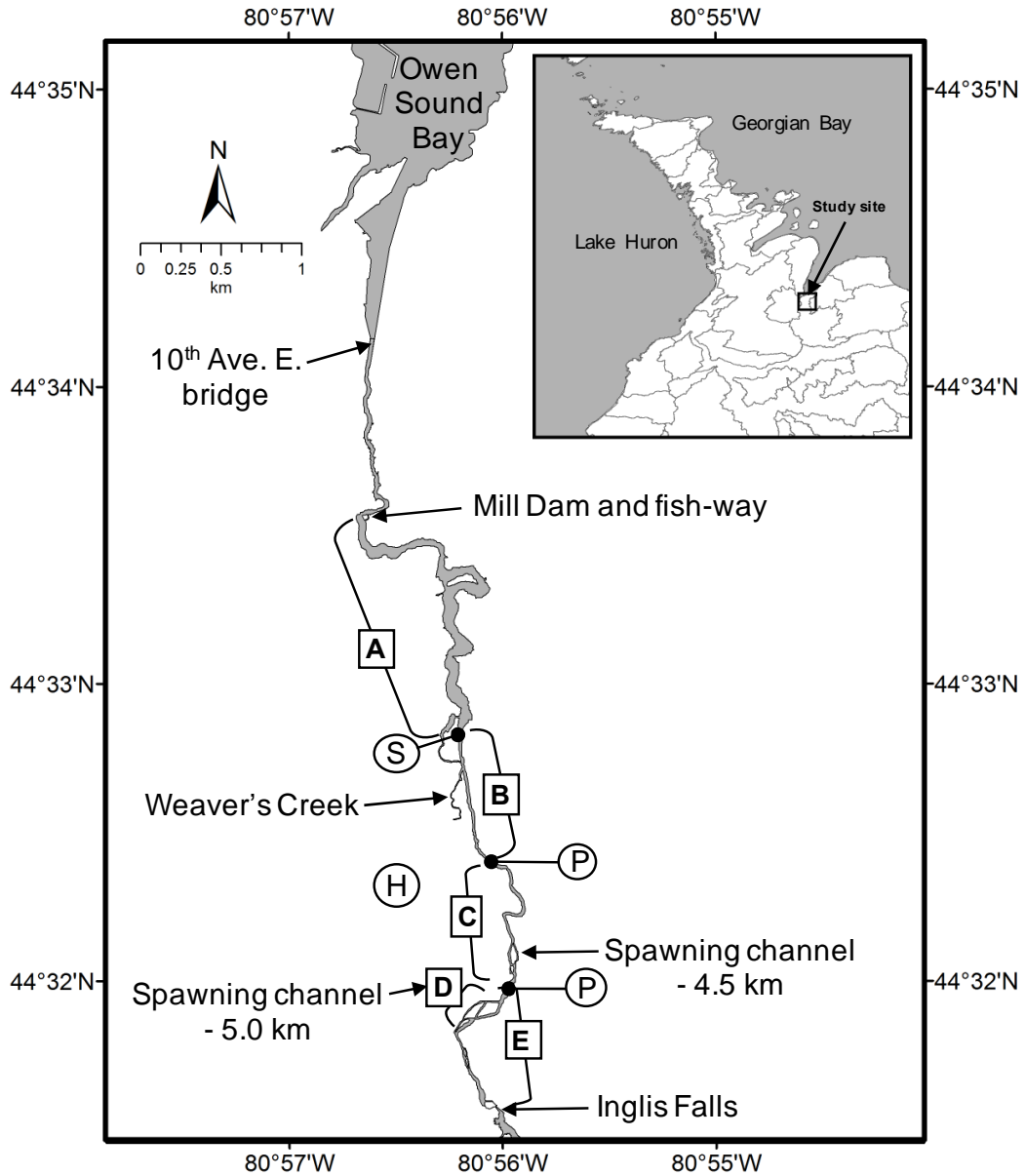


Figure 2.1: Map of the Sydenham River (Owen Sound, Ontario) accessible to spawning Chinook salmon. Locations of PIT tag antenna arrays (P), the Sydenham Sportsmen's Association's hatchery (H) and stocking site (S) are indicated in circles. Monitored river sections: A) reservoir area, B) 3 km spawning channel, C) middle river, D) spawning channel at river km 5.0, and E) upper river are indicated in boxes. The insert map shows tertiary watersheds and the study site situated in southern Georgian Bay.

The length of trap deployments ranged from 8 min to 24 h (average 7.5 h). Operation of the fish-trap was adjusted to minimize stress on captured fish and varied with the rate of fish migrating upstream. The fish-trap was generally deployed overnight (between 1800 h and 0800 h) except when the rate of fish migrating upstream was high. Deployment and retrieval of the fish trap was completed daily between 0800 h and 1800 h. Fish were not tagged while CFIP groups collected gametes, because consistent sampling of fish from the population for tagging could not be maintained. Enumeration of fish that migrated through the fishway continued during CFIP gamete collections. Sex and rearing-origin were identified for all fish captured in the fish-trap. Sex was determined visually (head and body shape) and by placing gentle pressure on the abdomen to feel or express gametes. Origin was determined by the absence (hatchery) or presence (naturalized) of an adipose fin. It was assumed that hatchery fish originated from the Sydenham Sportsmen Association's hatchery and naturalized fish originated from the Sydenham River. The next nearest Chinook salmon hatchery and stocking site was located in Port Elgin (Ontario), a distance of over 220 km for a fish to swim from the Sydenham River mouth. Ten males and ten females were targeted daily for tagging. If the fish-trap contained more than the target number of fish, individuals were selected haphazardly from the fish-trap basket using large dip nets. If less than the target number of fish were sampled after the first deployment, the fish-trap was re-deployed and sampled again later that day.

Fish selected to be tagged were immediately anesthetised in a solution of 20 mg/l clove oil in river water. Anesthetised fish were weighed to the nearest gram and fork lengths measured to the nearest millimetre. Secondary sexual traits (hump height and snout length) were measured to the nearest 0.1 mm for a few fish ($n = 22$) in 2010 and all fish in 2011. The date a fish was tagged was recorded as arrival date.

Fish were tagged with Peterson disc tags (Floy Tag Co., Seattle, WA) and half duplex passive integrated transponders (PIT tags) (Oregon RFID, Portland OR, www.oregonrfid.com). A 3.1 cm disc tag and a 32 mm PIT tag were used for fish greater than 2 kg, while a 2.2 cm disc tag and a 23 mm PIT tag were used for fish less than 2 kg. Nickel pins secured disc tags through the muscle immediately below the origin of the dorsal fin. Disc tags were color coded for easy visual identification of sex and rearing-

origin: hatchery female (light pink), naturalized female (green), hatchery male (blue) and naturalized male (yellow) and given unique alpha-numeric codes (e.g., AA, AB, AC) for individual identification. Uniquely coded PIT tags were surgically implanted into the abdomen between the pectoral and anal fins. To prevent infection and tag loss, 3M VetBond surgical adhesive (www.3M.com) was used to seal the incision. Tagged fish were held until they could maintain an upright swimming position in the recovery tank. Handling time was 5 - 10 min and time out of water did not exceed 3 min. Fish were released within 3 m of the upstream confluence to the fishway.

Attempts were made to minimize stress on individuals during tagging including: capturing fish using a fish-trap, minimizing numbers of fish held in the fish-trap, holding fish pre and post tagging fully immersed in flowing river water, and limiting handling time (Thorstad et al. 2013). While the effects of handling, clove oil anesthetization (Javahery et al. 2012), and intracoelomic surgical implantation of tags (Cooke et al. 2011) on fish movement and behavior are not fully understood, it is believed to be minimal and temporally limited (1 - 5 days) (Cooke et al. 2011; Gardner et al. 2015). Furthermore any potential effects from tagging should be minimal on my comparisons because all tagged fish were handled similarly. Procedures were approved by the Western University's Animal Use Subcommittee under Animal Use Protocol 2008-077.

2.2.3 Observations of fish in the river

Pre-spawning movements and spawning locations of tagged fish were determined using continuous monitoring by PIT antennas and daily shoreline surveys. PIT antenna arrays were constructed at river km-3.7 (lower array) and km-5.0 (upper array) (Figure 2.1). To acquire direction of movement, each array consisted of duplicate antennas, one position in pool habitat and one position approximately 20 m upstream in riffle habitat. All antennas were approximately 20 × 2 m in dimension and consisted of a double loop of 2.5 mm diameter copper wire. In each array, antennas were connected to stationary multi-antenna PIT readers (Oregon RFID) and powered by a 12V marine grade deep cycle battery. Antenna arrays were operational from 10 September to 29 September, 2010 and 6 September to 16 October, 2011, and were checked daily for proper operation and sufficient power supply. During 2010, technical issues including intermittent power

supply reliability and data logging errors resulted in a lack of usable data. In 2011, the system was continuously operational with the exception of one power interruption at the lower antenna array sometime between 25 September at 1917 h and 26 September at 1448 h.

In 2010 and 2011, shoreline surveys for tagged individuals were performed daily in river section B (river km-3.0 to km-3.7) and D (spawning channel at river km-5.0) between 0800 h and 2000 h (Figure 2.1). Shoreline surveys were not conducted in other areas of the river because the shoreline was not readily accessible. Similar to Gerson et al. (2016), three-minute behavioral observations were performed to identify tagged individuals and determine reproductive status: settled on nest(s) or not. Females were considered “settled” on a nest if nest defense (aggression towards males and other females), digging, or spawning behaviors (egg deposition) were observed. Once a female was determined to be settled, a shoreline GPS location was recorded and the site revisited each day for the remainder of her reproductive lifespan. Males were considered “settled” in an area if defensive (aggression towards other males or females) or spawning behaviors (quivering, head down behaviors, milt release) were observed. While males settle within a river section (e.g., 30 – 60 m in length), no GPS locations were recorded because many likely move frequently between nesting females within a section of river (Rich et al. 2006).

Shoreline surveys were also used to locate “newly dead” carcasses of tagged individuals. An individual was newly dead if the carcass had no signs of scavenging or decomposition or individuals had been observed alive the previous day. Reproductive lifespan was calculated as the number of days between arrival and death. Shoreline surveys were conducted from 10 September to 21 October, 2010 and 10 September to 17 October, 2011. In 2010, there were flow events with accompanying increases in water depth (+ 0.5 m) and turbidity which prevented visual observations of fish in the river between 22 – 24 and 26 - 28 September. In 2011, there were major flow events in the river on 23 – 26 September and 15 - 17 October. During these adverse conditions shoreline surveys for carcasses continued.

The last day a fish passed an antenna array or the first day a fish was observed settled in river section B or D was recorded as the date settled. Time to settled was

defined as the time period (days) from arrival date to date settled. Spawning location was assigned based on the last river section into which a fish moved or was visually observed to be settled. In cases where PIT antenna records indicated consistent passes of an antenna array over an average sex-specific reproductive lifespan of a fish, it was assumed the fish settled near that antenna array on the first date of the series of passes, with spawning location assigned to the river section in which the fish spent the majority of the time. Cross comparisons were made for females with PIT antenna records and visual observations of spawning locations ($n = 38$); no contradictions in assigned spawning locations were observed. Given the higher mobility of males than females, no unexpected contradictions were observed in males with antenna records and visual observations ($n = 101$). Spawning locations were assigned to the same river section for 80% of males with assignments of the remaining males (20%) within neighboring river sections. Differences likely occurred because males were visually observed near the end of a river section, but were settled and moving within an area overlapping two river sections. PIT antenna records of spawning locations were used for all further analysis in these cases. Fish without PIT antenna records or visual observations were minimal ($n = 4$; one female and three males) and excluded from further analysis because it could not be determined if they spawned in river section A, below the dam (although not observed), or died prior to spawning.

In 2011, observations from the PIT antennas were used to determine pre-spawning movements and calculate swim speed and upstream migration rate. Pre-spawning movement was defined as the series of broad scale movements prior to an individual settling in a river section to spawn. Pre-spawning movements were coded based on an individual's sequence of antenna crossings. Figure 2.2 presents the coding for a sequence of antenna crossings up to "pre-spawning movement 5," behavior coding continues in this pattern to a maximum of "pre-spawning movement 16." Pre-spawning movement 2 indicated an individual had moved upstream then back downstream past the lower antenna array without moving past the upper antennas; movement consistent with backtracking behavior predicted by the Johnsen-Quinn (2005) model for fish directly homing to the stocking site in river section B. Swim speeds and upstream migration rates were calculated as relative rates (body lengths/s) and absolute rates (km/day) from the initial upstream passes of the antenna arrays. Swim speed was calculated to test for

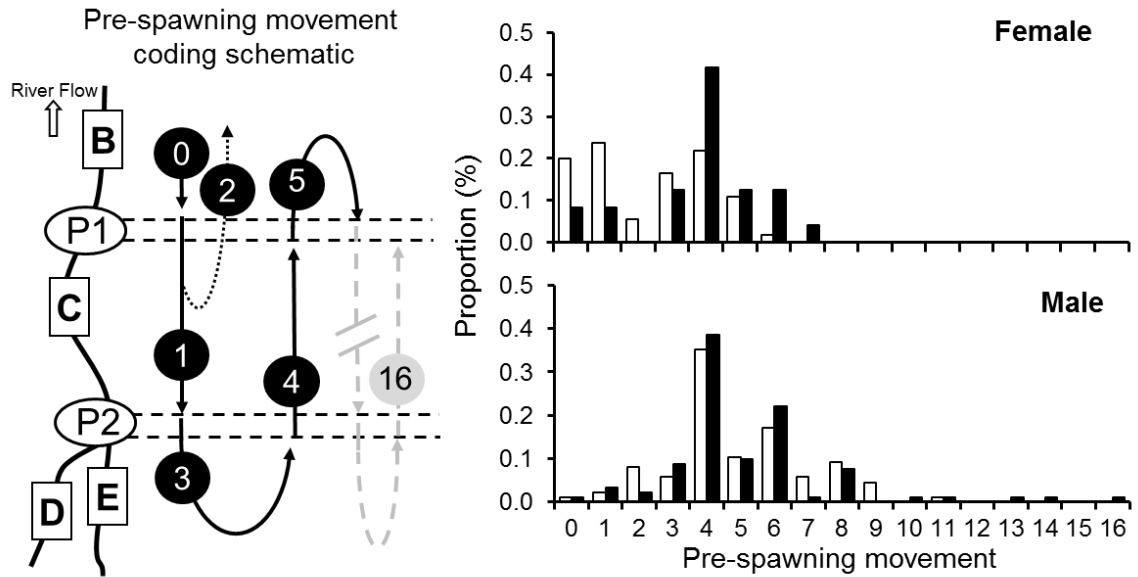


Figure 2.2: Pre-spawning movements of Chinook salmon in the Sydenham River. A schematic of how pre-spawning movements are coded from PIT antenna records is presented on the left. A stylized Sydenham River study setup is presented with monitored river sections (B – E) indicated in boxes and antenna arrays (P1 and P2) indicated with ovals. Dashed lines extending from antenna arrays represent the duplicate antennas. Solid lines with arrows represent direction of fish movement with intercepts between solid lines and the antennas indicating antenna crossings. Pre-spawning movement codes are indicated in circles. Pre-spawning movement 2 was consistent with backtracking presented in the Johnsen-Quinn (2005) model of natal homing (indicated by dotted black line). Coding following the 1-3-4-5 sequence to a maximum of 16 (represented by a broken, grey dashed line). On the right side are histograms (%) by sex and rearing-origin of pre-spawning movements displayed by tagged fish in 2011; hatchery fish (open bars), and naturalized fish (close bars).

differences in swimming abilities between rearing-origins from the transit times between the two antennas in the lower antenna array (20 m). Upstream migration rates were calculated because it may indicate differences in lateral, exploratory movements during upstream migration. Upstream migration rate was calculated from the transit time between the lower and upper antenna arrays (1170 m).

2.2.4 Statistical analysis

Hatchery fish may differ phenotypically from naturalized fish, which potentially confounds habitat use analysis (Foote, 1990; Knudsen et al. 2006, 2008; Schroder et al. 2008, 2010, 2012). Prior to analysis of pre-spawning movements and spawning distributions, one-factor MANOVAs were used to test for differences in phenotypic traits between rearing-origins within sexes in 2010 (length, weight) and 2011 (length, weight, hump height, and snout length). For comparison, secondary sexual traits were divided by fork length to control for fish size but results are presented relative to average sex-specific fork lengths within years. Significant MANOVAs were followed by one-factor ANOVAs to determine which individual phenotypic traits differed between rearing-origins. In 2010, only univariate ANOVAs were used to test for differences in secondary sexual traits (hump height and snout length) between rearing-origins because these traits were not measured on all fish. This approach maintained the highest possible sample sizes for comparisons of each trait and minimized the probability of a type one error (Tabachnick and Fidell, 2007).

Habitat use was analysed independently for the sexes because previously studies have demonstrated differences in the female and male mating systems including, protandry (e.g., Morbey 2000), pre-spawning movements (e.g., Anderson et al. 2007), and the accuracy and precision of natal homing (e.g., Neville et al. 2006). Poisson (log-linear) regression analysis was used to test differences in the extent of pre-spawning movement between rearing-origins within sexes during 2011. Poisson regression models to test the effects of rearing-origin, arrival timing and phenotypic traits (length, weight, hump height, and snout length) on the extent of pre-spawning movement were developed independently for each sex. A backwards, stepwise approach and Akaike Information Criterion (AIC) were used to select the combination of variables that produced optimal

model performance. To adjust for overdispersion, models were scaled using the Pearson Chi-square statistic. Subsequently, logistic regression analysis was used to explicitly determine the probability of tagged fish displaying direct homing to the stocking site (river section B). Pre-spawning movements were grouped into two groups to create a binary response variable. Group one included pre-spawning movements ≤ 2 (Figure 2.2); behaviors consistent with the Johnsen-Quinn (2005) model for fish directly homing to the stocking site (i.e., fish that moved < 1.8 km after passing the stocking site). Group two included pre-spawning movements ≥ 3 (Figure 2.2) or fish that moved > 1.8 km after passing the stocking site. The development of logistic regression models used the same predictor variables and approach as the Poisson regression analysis. For fish tagged in 2011, univariate one-factor ANOVAs were used to test differences in swim speed and upstream migration rate between rearing-origin within sexes.

In 2010, two 2×3 contingency Chi-square tests (χ^2) were used to test independence of spawning location (river sections B and D, and fish not re-observed) with rearing-origin within sexes. In 2011, two, 2×4 contingency Chi-square tests were used to test independence of spawning location (river sections B, C, D, and E) with rearing-origin within sexes. Additionally in 2011, a series of pairwise two-sample Kolmogorov–Smirnov ($K-S$) tests were also used to test for differences within sexes in distributions of settling dates among river sections, and between rearing-origins within river sections.

The daily numbers of Chinook salmon returning to spawn above the Mill Dam were estimated using daily capture rates in the fish-trap with modified equations from Hurbert and Fabrizio (2007). The number were estimated using the equation:

$$N_{ijk} = (C_{ijk} / f_k \cdot q) * 24$$

Where C_{ijk} is the number of fish caught from origin i and sex j on day k , f_k is the total length of trap deployment (hours) on day k , and q is the catchability coefficient. The equation was multiplied by 24 (hours) to produce a daily estimate. The catchability coefficient was set to one (i.e., $q = 1$), because it was assumed all fish moving upstream were captured during fish-trap deployment. The total numbers of fish by sex and rearing-origin were estimated from the summation of daily estimates ($N_{ij} = \sum N_{ijk}$). Arrival timing, time to settle and reproductive lifespan were analysed independently for the sexes

because previously studies have demonstrated salmonids can show protandry or earlier arrival of males than females on spawning grounds (Morbey 2000).

Median arrival date defined as the day when the cumulative percent of fish to have arrived (cumulative arrival distribution) exceeded 50%, was used as a descriptive statistic instead of mean arrival date because arrival distributions were episodic and not normally distributed. Arrival timing bias between rearing-origins was estimated from the slope in the line of the proportion of hatchery fish arriving each day to date. For example, a positive slope would indicate a bias towards later arrivals of hatchery fish than naturalized fish. For fish tagged in 2011, univariate one-factor ANOVAs were used to test differences in time to settle and reproductive lifespan within sexes and between rearing-origin. All statistics were performed using SAS Version 9.3.

2.3 Results

In 2010, there were no differences in phenotypic traits (length, weight) between rearing-origins in females (MANOVA: *Wilks* $\lambda = 0.97$, $F_{2,65} = 0.97$ $p = 0.39$; Table 2.1) but there were in males (MANOVA: *Wilks* $\lambda = 0.94$, $F_{2,144} = 4.44$ $p = 0.01$). The mean weight of naturalized males in 2010 was less than hatchery males (Table 2.1). In 2011, there were no differences in phenotypic traits (length, weight, hump height, and snout length) between rearing-origins in females (MANOVA: *Wilks* $\lambda = 0.91$, $F_{4,75} = 1.75$ $p = 0.15$; Table 2.1) but there were in males (MANOVA: *Wilks* $\lambda = 0.92$, $F_{4,176} = 3.98$ $p = 0.004$). In 2011, naturalized fish had a shorter mean length and a taller mean hump height for their length than hatchery fish (Table 2.1). Because of these results, I incorporated phenotypic traits, sex and rearing-origin as covariates in the analysis of pre-spawning movement and spawning distributions.

In 2011, hatchery females appeared to have less extensive pre-spawning movements than naturalized females (Figure 2.2). Most naturalized females (71%) migrated past both antenna arrays before moving back downstream to settle on spawning locations (pre-spawning movement ≥ 4). Most hatchery females (65%) settled during their initial upstream migration (pre-spawning movement ≤ 3).

Table 2.1: Phenotypic trait comparisons between rearing-origins of female and males Chinook salmon in the Sydenham River. Results presented as mean \pm standard error with univariate one-factor ANOVA comparisons. Secondary sexual traits (hump height and snout length) are presented as averages relative to the population mean fork length (2010 = 70.3 cm; 2011 = 70.7 cm). Sample size for univariate comparisons are presented in brackets if smaller than the total number of tagged fish.

Trait	Year	Female				Male			
		Hatchery (H)	Naturalized (N)	ANOVA		Hatchery (H)	Naturalized (N)	ANOVA	
N	2010	44	24			92	55		
	2011	55	25			88	93		
Length (cm)	2010	75.0 \pm 1.0	74.4 \pm 1.7	$F_{1,66} = 0.14$	H = N	69.7 \pm 0.6	65.9 \pm 1.4	$F_{1,145} = 7.99$	H = N
	2011	75.5 \pm 0.8	73.5 \pm 1.2	$F_{1,78} = 1.69$	H = N	70.5 \pm 1.2	67.2 \pm 1.0	$F_{1,179} = 4.3^*$	H > N
Weight (kg)	2010	5.14 \pm 0.22	5.33 \pm 0.28	$F_{1,66} = 0.28$	H = N	3.94 \pm 0.13	3.33 \pm 0.18	$F_{1,145} = 8.57^*$	H > N
	2011	5.07 \pm 0.21	4.85 \pm 0.24	$F_{1,78} = 0.38$	H = N	4.16 \pm 0.19	3.80 \pm 0.17	$F_{1,179} = 2.0$	H = N
Hump height (mm)	2010	66.6 \pm 4.3 (n = 4)	- (n = 0)	-	-	77.5 \pm 2.2 (n = 8)	77.3 \pm 2.6 (n = 10)	$F_{1,16} = 0.00$	H = N
	2011	70.2 \pm 0.6	72.3 \pm 1.1	$F_{1,78} = 3.34$	H = N	77.6 \pm 0.5	80.1 \pm 0.7	$F_{1,179} = 8.3^*$	H < N
Snout length (mm)	2010	66.3 \pm 4.5 (n = 4)	- (n = 0)	-	-	76.2 \pm 1.8 (n = 8)	73.7 \pm 1.9 (n = 10)	$F_{1,16} = 0.88$	H = N
	2011	64.4 \pm 0.5	65.8 \pm 0.8	$F_{1,78} = 2.62$	H = N	80.6 \pm 0.5	79.7 \pm 0.6	$F_{1,179} = 1.1$	H = N

* $p < 0.05$

Poisson regression analysis of female pre-spawning movements resulted in a model (intercept = - 382.9) with significant effects of arrival date (0.02: Wald X^2 = 7.50, df = 1, P = 0.006), fish length (- 0.04: Wald X^2 = 9.18, df = 1, p = 0.002) and rearing-origin (- 0.37: Wald X^2 = 6.13, df = 1, p = 0.01). These results indicated the extent of pre-spawning movement increased with later arrival dates, decreased with fish length, and was lower in hatchery than in naturalized females. The logistic regression analysis of pre-spawning movement with direct natal homing to the stocking site also resulted in significant effects of arrival date (- 0.07: Wald X^2 = 6.00, df = 1, p = 0.01), fish length (0.11: Wald X^2 = 5.01, df = 1, P = 0.03), and rearing -origin (0.75: Wald X^2 = 5.49, df = 1, p = 0.02; Figure 2.3). This indicated that hatchery fish were more likely to display direct natal homing behaviours to the stocking site. Swim speed of females were mean \pm standard error (SE) 0.34 ± 0.03 body lengths/s (22 ± 2 km/day) with upstream migration rates of 0.056 ± 0.005 body lengths/s (3.5 ± 0.3 km/day) and no difference between rearing-origins (Table 2.2).

In 2011, males regardless of rearing-origin performed extensive pre-spawning movement throughout the river prior to settling (Figure 2.2). Eighty-four percent of males continued to move after their initial upstream pass of the river (pre-spawning movement ≥ 3). Thirty-seven percent of males continued to move after the initial up and downstream pass of the river (pre-spawning movements > 5), with 17% performing at least a complete second upstream pass (pre-spawning movements > 7). One male performed just over six complete passes of the river before settling (pre-spawning movement 16). Poisson regression analysis of pre-spawning movement resulted in an intercept only movement model (intercept = 1.60) indicating that rearing-origins, arrival date, and phenotypic traits (i.e., length, weight, hump height, snout length) were not good predictors of the extent of male pre-spawning movement. The logistic regression analysis of pre-spawning movement with direct natal homing to the stocking site also resulted in an intercept only model: $\log(P_i/1-P_i) = 2.3$ (Wald X^2 = 78.6, df = 1, p < 0.001). Swim speed of males was mean \pm SE 0.50 ± 0.03 body lengths/s (29 ± 2 km/day) with upstream migration rates of 0.083 ± 0.003 body lengths/s (4.9 ± 0.2 km/day) and no differences between rearing-origins (Table 2.2).

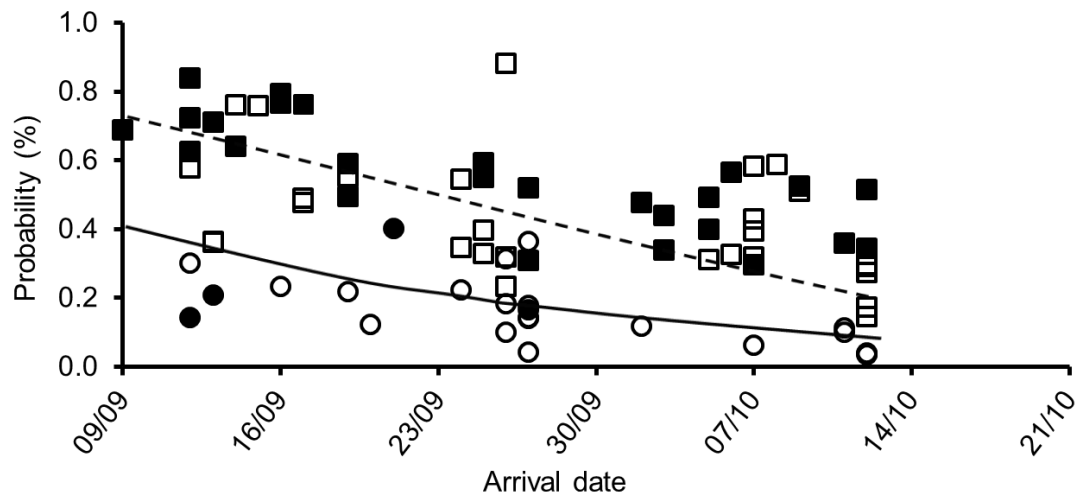


Figure 2.3: Probability that female Chinook salmon in the Sydenham River directly homed to the stocking site in 2011. Lines represent logistic regression curves for hatchery (dashed line) and naturalized (solid line) females. Symbols indicate the predicted probability of individual hatchery (square) and naturalized (circles) females displaying direct homing to the stocking site based on body length standardized mean female length (74.7 cm), arrival date and rearing-origin (i.e., the logistic regression model). Closed symbols indicate individuals with observed direct homing to the stocking site (pre-spawning movement ≤ 2 ; Figure 2.2); open symbols indicate individuals with other pre-spawning movements (pre-spawning movement > 3).

Table 2.2: Re-sighting rate, swim speed, time to settle and reproductive lifespan comparisons between rearing-origins within sexes of tagged Chinook salmon in the Sydenham River (Owen Sound, ON) in 2010 and 2011. Where applicable results presented as mean \pm standard error with univariate ANOVA comparisons. Sample size for univariate comparisons presented in brackets.

Trait	Year	Females			Males		
		Hatchery (H)	Naturalized (N)	ANOVA	Hatchery (H)	Naturalized (N)	ANOVA
% Re-sighted	2010	0.45	0.21		0.53	0.54	
	2011	1.0	0.96		0.99	0.99	
Median arrival date	2010	Oct 1	Oct 3		Oct 2	Oct 2	
	2011	Oct 10	Sep 26		Sep 28	Sep 28	
Short distance swim speed							
body length \cdot s ⁻¹		0.32 \pm 0.03	0.37 \pm 0.06	F _{1,59} = 0.78	0.46 \pm 0.03	0.53 \pm 0.05	F _{1,166} = 1.80
[km \cdot day ⁻¹]	2011	[20.5 \pm 1.9]	[23.3 \pm 3.6]	H = N	[27.6 \pm 2.0]	[30.3. \pm 2.9]	H = N
		(n = 39)	(n = 22)		(n = 83)	(n = 85)	
Long distance swim speed							
body lengths \cdot s ⁻¹		0.056 \pm 0.006	0.056 \pm 0.006	F _{1,43} = 0.00	0.089 \pm 0.005	0.078 \pm 0.004	F _{1,146} = 2.62
[km \cdot day ⁻¹]	2011	[3.5 \pm 0.3]	[3.5 \pm 0.3]	H = N	[5.2 \pm 0.3]	[4.5 \pm 0.3]	H = N
		(n = 26)	(n = 19)		(n = 72)	(n = 76)	
Time to settled (days)	2011	3.9 \pm 0.5	4.8 \pm 0.9	F _{1,77} = 0.68	4.6 \pm 0.4	5.0 \pm 0.4	F _{1,176} = 0.58
		(n = 55)	(n = 24)	H = N	(n = 87)	(n = 91)	H = N
Reproductive lifespan (days)	2011	9.3 \pm 1.0	10.8 \pm 2.2	F _{1,20} = 0.36	14.6 \pm 1.1	13.6 \pm 1.1	F _{1,33} = 0.64
		(n = 18)	(n = 4)	H = N	(n = 19)	(n = 17)	H = N

*0.0001 < p < 0.05

In 2010, there were no significant differences in proportions of hatchery and naturalized females ($X^2 = 4.5$, $df = 3$, $p = 0.11$) and males ($X^2 = 0.4$, $df = 2$, $p = 0.82$) settling to spawn in river section B and D (Figure 2.4). In 2011, despite observed differences in the extent of pre-spawning movement between rearing-origins in females, tagged fish spawned throughout the monitored river sections with no differences in proportions of hatchery and naturalized fish settling in river sections B – E for females (Figure 2.4; $X^2 = 0.6$, $df = 3$, $p = 0.90$) and males (Figure 2.4; $X^2 = 5.4$, $df = 3$, $p = 0.14$). The highest densities of tagged females spawned in river section B (34 females/river km), then C (23 females/river km), E (16 females/river km) and D (10 females/river km). For females there was a difference between distributions of settling dates in river sections C and E (Figure 2.5; *K-S* test: $0.21 D = 0.46$, $p = 0.02$), but other pairwise comparisons were not significant (Figure 2.5; *K-S* test: $p > 0.05$) and there were no differences between rearing-origins within each river section (Figure 2.5; *K-S* tests: $p > 0.05$). The highest densities of tagged males spawned in river section B (74 males/river km), then D (68 males/river km), then C (38 males/river km) and finally E (35 males/river km). Males displayed no differences in distributions of settling date among the river sections (Figure 2.5; *K-S* tests: $p > 0.05$) or between rearing-origins within river sections (Figure 2.5; *K-S* tests: $p > 0.05$).

Had analysis of spawning distributions been based on carcass recovery as done by other studies (e.g., Hoffnagle et al. 2008, Dittman et al. 2010) results would have been different. In 2011, 83% of female carcasses that were recovered ($n = 23$), were recovered in the river section where they were observed settled, 17% were recovered in the section immediately below. Forty-seven percent of male carcasses that were recovered ($n = 34$) were recovered in the river section where they settled, 29% were recovered in the section immediately below and 6% in other river sections below. I also recovered 18% of male carcasses above the river section in which they settled.

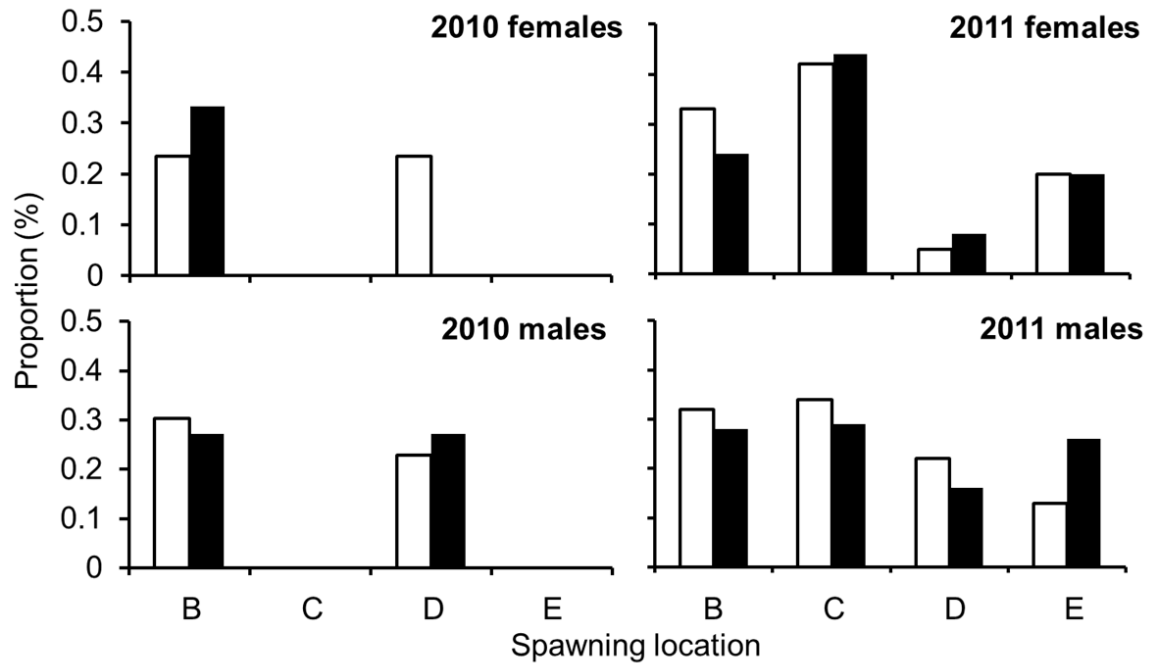


Figure 2.4: Proportions by sex and rearing-origin of tagged Chinook salmon settled to spawn in sections B - E of the Sydenham River in 2010 and 2011. Open bars represent hatchery fish and solid bars represent naturalized fish. River section A was not directly monitored, see Figure 2.1 for locations of river sections B - E.

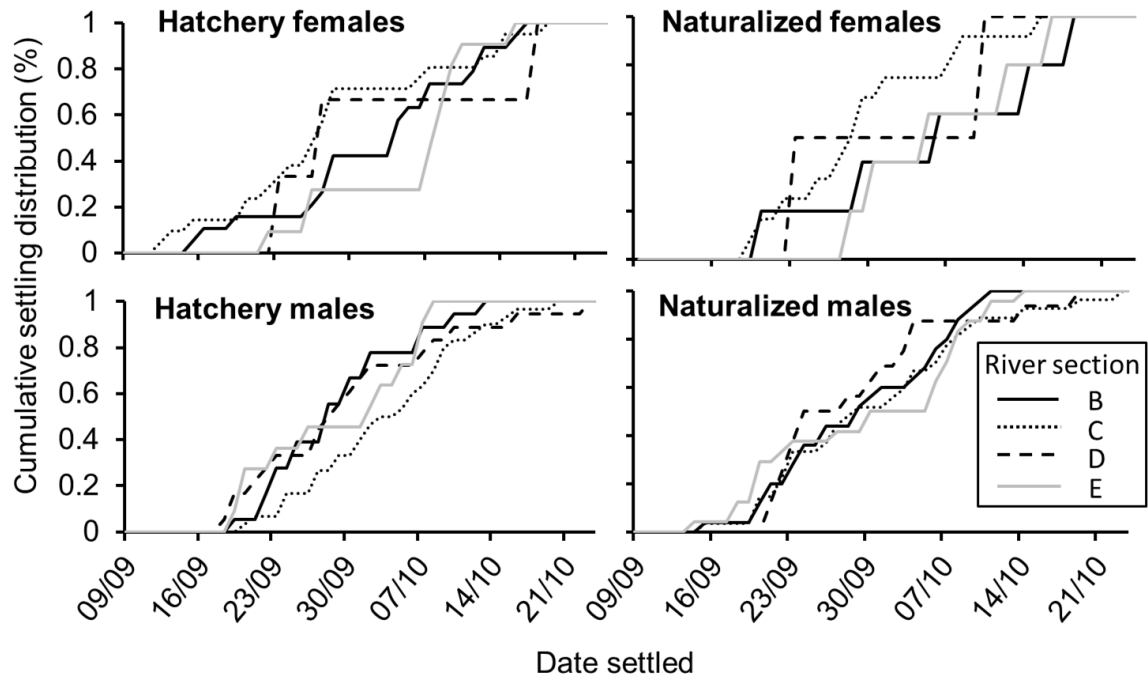


Figure 2.5: Cumulative settling distribution by sex and rearing-origin of Chinook salmon in sections B - E of the Sydenham River during 2011 (see Figure 2.1 for locations of river sections B - E).

In 2010, an estimated 3,219 Chinook salmon migrated upstream past the Mill Dam to spawn from 12 September to 14 October (Table 2.3; Figure 2.6). For females, the median arrival date was 2 October with no arrival timing bias ($t_{25} = -0.56$, $p = 0.60$, $r^2 = 0.01$; Figure 2.7). For males, the median arrival date was 2 October and there was no arrival timing bias ($t_{30} = 0.39$, $p = 0.70$, $r^2 = 0.005$).

In 2011, an estimated 3,305 fish spawned above the Mill Dam from 9 September to 14 October (Table 2.3; Figure 2.6). For females, the median arrival date was 7 October with no significant arrival timing bias ($t_{23} = 0.44$, $p = 0.66$, $r^2 = 0.009$; Figure 2.7). For males, the median arrival date was 28 September for both rearing-origins (Table 2.3) and there was no arrival timing bias ($t_{28} = -0.86$, $p = 0.40$, $r^2 = 0.03$; Figure 2.7). Females took mean \pm standard error 4.2 ± 0.5 days from arrival until they settled to spawn and had reproductive lifespan of mean \pm SE 10 ± 1 days; there were no differences in either timing trait between rearing-origins (Table 2.2). Males took mean \pm SE 4.8 ± 0.3 days from arrival until they settled in a river section to spawn and had reproductive lifespans of mean \pm SE 14 ± 1 days; there were no differences in either timing trait between rearing-origins (Table 2.2).

Table 2.3 Summary of estimated population size (*N*), arrival distribution and median arrival date by sex and rearing-origin in Sydenham River Chinook during 2010 and 2011.

Year	Trait	Female		Male	
		Hatchery	Naturalized	Hatchery	Naturalized
2010	<i>N</i>	270	214	1586	1149
	Arrival distribution	13 Sept - 14 Oct	20 Sept - 12 Oct	13 Sept - 14 Oct	12 Sept - 14 Oct
	Median arrival date	1 Oct	3 Oct	Oct 2	Oct 2
2011	<i>N</i>	339	197	1369	1400
	Arrival distribution	9 Sept - 14 Oct	12 Sept - 13 Oct	9 Sept - 13 Oct	12 Sept - 14 Oct
	Median arrival date	Oct 10	Sep 26	Sep 28	Sep 28

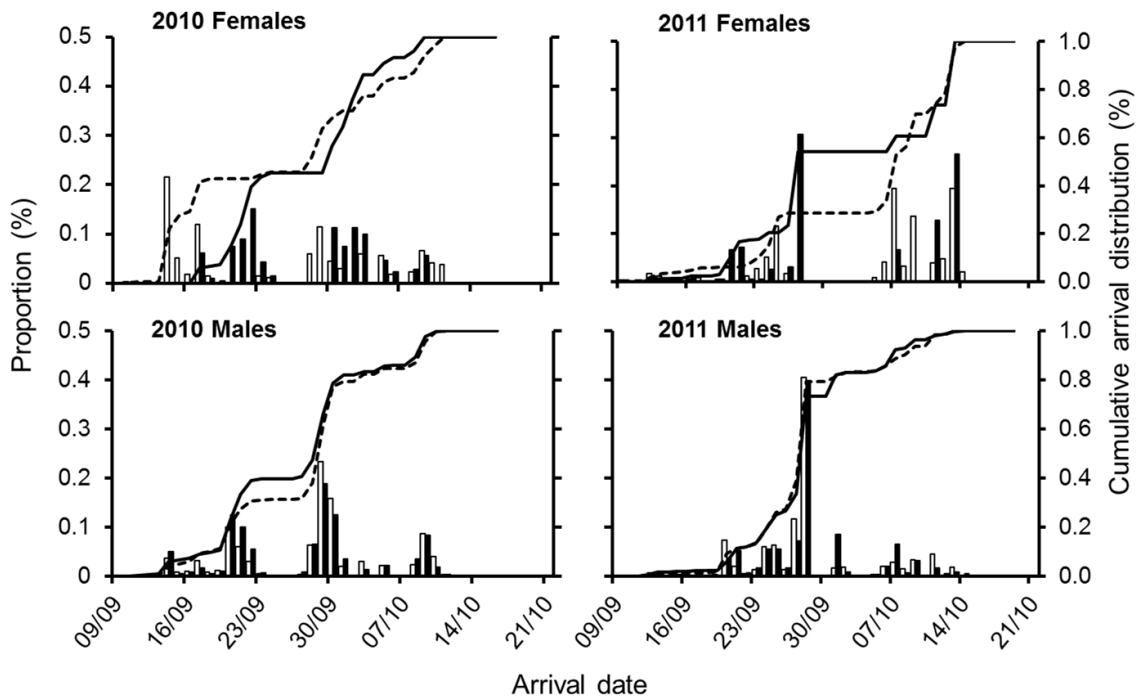


Figure 2.6: Distributions of arrival dates by sex and rearing-origin of Chinook salmon returning to spawn in the Sydenham River in 2010 and 2011. Open bars represent hatchery and closed bars represent naturalized fish. Cumulative arrival distributions (% of population to arrive by date) are indicated for hatchery fish (dashed lines) and naturalized fish (solid lines). Bars represent proportions of total estimated populations size but actual samples sizes of observed fish were: females (2010 = 98, 2011 = 106); and males (2010 = 474, 2011 = 400).

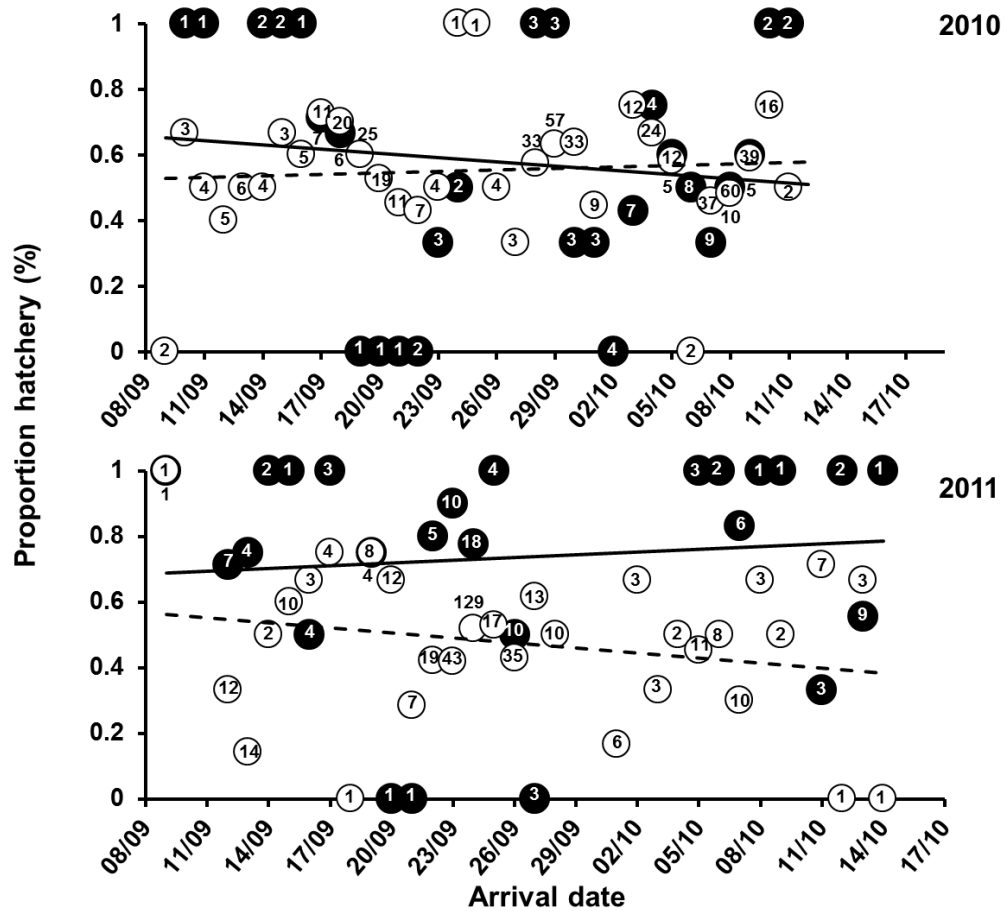


Figure 2.7: Proportion of hatchery fish (%) arriving by date in the Sydenham River in 2010 and 2011. Symbols represent proportion of hatchery females (closed) and males (open) arriving each day. Lines represent the linear regression for proportion of hatchery females (solid line) and males (dashed line) arriving with date. A significant positive slope would indicate arrival timing bias for earlier arrivals of hatchery fish; a negative slope for later arrival of hatchery fish. No slopes are significantly different than zero ($p = 0.05$). Number inside symbols represent sample size by date and sex, if graph elements overlap for clarity female sample sizes are displayed below and males above symbols

2.4 Discussion

Hatchery and naturalized Chinook salmon spawning in the Sydenham River showed no evidence of reproductive isolation in 2010 or 2011. Similarities in spawning distributions demonstrated a lack of reproductive isolation-by-distance and similarities in arrival timing, time to settle and reproductive lifespan demonstrated a lack of reproductive isolation-by-time. Further, when hatchery and naturalized Chinook salmon are present together on spawning grounds, research suggests they do not assortatively pair based on rearing-origin (Schroder et al. 2010). This suggests a high likelihood of interbreeding between hatchery and naturalized fish and that fish in the Sydenham River are functionally a single population.

Consistent with my predictions, I found hatchery females had limited pre-spawning movement upstream of the stocking site, resulting in less extensive pre-spawning movement than naturalized females. Forty-four percent of hatchery females settled directly to locations within 1.3 km of the stocking site (pre-spawning movement ≤ 1), compared to 17% of naturalized females. An additional 5% of hatchery females displayed backtracking behavior into the river section containing the stocking site (pre-spawning movement 2; Figure 2.2); a behavior not observed in any naturalized females. Similarities in swim speeds (i.e., swimming abilities) or upstream migration rates (i.e., lateral upstream movements) provide no alternative explanation for the differences between rearing-origins. Thus, findings are consistent with the pre-spawning movement predicted by the Johnsen–Quinn (2005) model and demonstrate similar homing precision in females (≈ 1 km) as Neville et al. (2006).

In addition to rearing-origin, body length and arrival date were important determinants of the extent of pre-spawning movement in females, with more extensive movements by later arriving and smaller individuals. These findings suggest increasing pre-spawning movement in response to despotic behaviors among females. Foote (1990) found that earlier settling and larger female Kokanee Salmon (nonanadromous *O. nerka*) excluded newly arriving females of similar or smaller size from nesting sites. Female Coho Salmon (*Oncorhynchus kisutch*) showed a similar size advantage in territorial behaviours (van den Berghe and Gross, 1989). As semelparous, capital breeders, female salmon must balance energy requirements prior to spawning including pre-spawning

movements during upstream migration and intrasexual competition for spawning sites with the energy required for spawning and post-spawning nest defense (Fleming and Reynolds 2004). Consistent with these tradeoffs, later arriving female Sockeye Salmon have been observed spawning in poor quality habitat with lower densities of spawning salmon (Adkison et al. 2014).

In contrast to females, males displayed extensive movements up and down the 3.5 km of spawning habitat in the Sydenham River, and the extent of pre-spawning movement was independent of rearing-origin, arrival timing, and phenotypic traits. Anderson et al. (2007) also found no relationship between the extent of pre-spawning movement and arrival date or fish length in male Coho Salmon. In this study, individuals travelled a total distance six times greater (45 km) than the linear river distance. Male Atlantic Salmon also display similar extensive pre-spawning movements with distances travelled 2-3 times greater (22.8 - 30.9 km) than the linear river distance (Økland et al. 2001). Male Chinook salmon invest less energy directly into reproduction (i.e., gamete production) or parental care (i.e., nest defense) than females, which likely allows for more energy to be allocated to finding spawning opportunities (Fleming and Reynolds, 2004). Hence, males likely use natal homing to get them to a general area within a river, then perform extensive movements over a defined area to evaluate potential spawning locations and mating opportunities.

The differences between my female and male pre-spawning movement models demonstrate pre-spawning movements consistent with the sex-specific roles of spawning salmonids. These behavioral observations also support sex-specific homing precision based on genetic analysis (Neville et al. 2006). My findings suggest that to minimize the interbreeding of hatchery and wild (or naturalized) fish, if that is desired, hatchery supplementation programs could promote natal homing of hatchery females to specific sites but it would be difficult to limit the movements of hatchery males.

Although I found differences in pre-spawning movement between hatchery and naturalized fish in the Sydenham River, there were no differences in spawning distributions between hatchery and naturalized fish of either sex. This contrasts previous studies (Mackey et al. 2001; Garcia et al. 2004; Dittman et al. 2010; Hoffnagle et al. 2008), including a study of introduced Chinook salmon in the Salmon River (New York,

US) (Nack et al. 2011). One explanation for the differences in my findings to previous research is simply that natal homing does not function on the spatial scale of suitable habitat in the Sydenham River ($\approx 3.5\text{km}$). However, this cannot be the entire story because pre-spawning movements did differ between hatchery and naturalized females.

My results suggest that individual site selection was also important in determining the observed spawning distributions. While homing gets fish to suitable spawning habitat, it eventually yields to individual spawning site selection based on favorable environmental and social conditions (Healey, 1991; Quinn, 2005). For example, Cram et al. (2013) found stocking location to be a major determinant of spawning location for hatchery Chinook salmon, but if habitat (e.g., substrate, cover, and channel type) near stocking sites was not suitable, females strayed to spawning in higher quality habitat elsewhere. Based on the logic from Hendry et al. 2001 (i.e., females settle in the highest quality habitat first and at the highest densities), my results suggest that suitable spawning habitat was likely present in all river sections (B – E) with slightly higher quality habitat occurring in river sections B and C. Intrasexual competition among females for nesting sites also influences site selection, and Chinook salmon populations show density-dependent spawning distributions consistent with the ideal despotic (pre-emptive) distribution (Fretwell and Lucas, 1970; Falcy, 2015). My results of increasing pre-spawning movements with arrival date is consistent with density-dependent movement. Moreover, Gerson et al.'s (2016) findings of high rates of egg retention and nest superimposition provide evidence of active density-dependent mechanisms among females (Kinnison et al. 1998; Quinn et al. 2007; Schroder et al. 2008). In the Sydenham River, the approximately 3.5 km of suitable habitat may simply be too limited given the numbers of returning females (2010 = 484; 2011 = 536), with the best habitat occurring close to the stocking site (sections B and C), for spawning distributions to differ between rearing-origins. Moreover, once females are distributed across suitable habitat, males should follow suit. My observations suggest that a comparison of spawning distributions alone will not provide a complete assessment of how habitat use between hatchery and naturalized fish differ.

In my study, artificial selection on arrival and spawning timing was probably weak and likely would not differ in intensity between hatchery and naturalized fish. Hatchery

and naturalized fish in the Sydenham River demonstrated a lack of differences in arrival time, time to settle, and reproductive lifespan. Similarly, Kern et al. (2016) found no difference in arrival timing between hatchery and naturalized Chinook salmon in Lake Michigan tributaries. These findings in the Great Lakes seem inconsistent with a growing body of literature demonstrating differences between rearing-origins. For example, within a single generation, hatchery Chinook salmon in the upper Yakima River (Washington, US) showed no overall difference in median arrival date, but spawned an average of 5.1 days earlier than wild fish over four years (Knudsen et al. 2006). Another 16-year study in the Imnaha River (Oregon, US) found that wild Chinook salmon consistently arrived and spawned earlier than hatchery fish (Hoffnagle et al. 2008). However, while gamete collections were consistent relative to calendar date, this does not mean they were consistently early or late relative to the arrival distribution of the population. Moreover, hatchery fish are not targeted for gamete collection, and so hatchery and naturalized fish are not reproductively isolated in the hatchery or in the river.

Artificial selective pressures from hatchery programs can shift arrival and spawning timing away from favorable temperature regimes (Quinn et al. 2002). Moreover, modelling has shown that prolonged and intensive stocking into an Atlantic Salmon *Salmo salar* population perpetuated a phenological mismatch and increased risks of climate-mediated extinction (McGinnity et al. 2009). In the Sydenham River, Gerson et al. (2016) suggested that intensive hatchery supplementation may have contributed to the weak phenological match between arrival timing and river temperature regimes documented in 2010 and 2011. Female salmon settled on spawning locations when river temperatures were above what is considered suitable ($> 12.8^{\circ}\text{C}$). The lack of reproductive isolation I observed would likely facilitate this process of artificial selection. A better understanding of arrival and spawning timing of Chinook salmon in the Great Lakes is becoming increasingly important for management as fisheries become sustained by naturalized populations and in light of potential shifts in temperature and flow-regimes forecasted by climate change scenarios. Chinook salmon in the Great Lakes provide a valuable resource for understanding how the interactions between hatchery practices and regional climate affect arrival and spawning timing, and could provide potentially

valuable information for salmonid stocking programs including protocols to aid the rehabilitation of threatened and endangered populations.

My individual level examination of habitat use and arrival timing found extensive use by hatchery and naturalized Chinook salmon of the accessible habitat in the Sydenham River and a lack of reproductive isolation between hatchery and naturalized fish. Evidence suggests the lack of difference in female spawning distributions was the result of the limited suitable spawning habitat (≈ 3.5 km), the proximity of the best spawning habitat to the stocking site, and despotic behaviours among females. Males likely matched the distribution of females. The lack of difference in arrival timing may be the result from weak artificial selection on arrival and spawning timing and the effects of the stocking program. These results have some important consideration for future management of Chinook salmon in the Great Lakes and other supplemented populations.

I suggest that the lack of reproductive isolation between hatchery and naturalized Chinook salmon may suppress contributions of naturalized fish from supplemented populations to the fishery. Reductions of reproductive success in hatchery Steelhead Trout have been reported to be 40% per generation with wild born offspring of hatchery parents displaying 12 % reductions with one hatchery parent or 62 % reductions with two hatchery parents, compared to fish with two wild parents (Araki et al. 2007, 2008, 2009). Consequently, prolonged and intensive stocking programs producing high numbers of returning hatchery fish can reduce the productivity of wild populations (Kostow and Zhou 2006; McGinnity et al. 2009; Chilcote et al. 2011). This raises two issues of importance for fisheries management. First, if promotion of naturalized strains of Chinook salmon adapted to the Great Lakes environmental conditions is desirable, river stocking should be limited to enable local adaptation to natural selective pressures and divergence of naturalized populations. This is a concept that should also be applied to restore salmon populations in native rivers. Secondly, alterations to stocking rates (i.e., reductions in stocking) or strategies (e.g., open water stocking instead of river stocking) in the Great Lakes may not result in a predictable response in the abundances in the fisheries as the hatchery influences are reduced or removed from supplemented naturalized populations.

I also suggest that extensive use of accessible river habitat by hatchery and naturalized Chinook salmon may have significant effects on the riverine ecosystems

throughout the Great Lakes. The presence of Chinook salmon in Great Lakes tributaries are associated with increased dissolved nutrients (soluble reactive phosphorous, dissolved organic carbon, ammonium and nitrate), elevated organic pollutants concentrations (e.g., polychlorinated biphenyls [PCBs], dichlorodiphenyldichloroethylene [DDE], and polybrominated diphenyl ethers [PBDEs]), decreased periphyton and macroinvertebrate abundance, and displacement of native species such as Brook Trout, *Salvelinus fontinalis* (Collin et al. 2011; Janetski et al. 2011, 2012, 2014). This also has two issues of importance for management of this introduced species. First, stocking in river may intensify these ecosystems effects within rivers as hatchery fish return and potentially increasing the numbers of spawning salmon in the rivers. Second, potential impacts of Chinook salmon on previously uncolonized river sections needs to be considered for habitat restoration projects restoring the connectivity between lake and riverine habits. The presence of Chinook salmon may be counteractive to the objective of such projects.

My study represents one of few (e.g., Carl, 1982; Kerr and Perron, 1986; Nack et al. 2011; Gerson et al. 2016; Kerns et al. 2016) to have examined the reproductive ecology of introduced Chinook salmon in the Great Lakes tributaries. As Chinook salmon fisheries in the Great Lakes become sustained primarily by naturalized populations, understanding factors influencing reproductive success and productivity of naturalized populations is becoming increasingly important. Future research should examine differences in reproductive success between hatchery and naturalized Chinook salmon, including differences in the arrival and spawning timing among populations with varying hatchery influences, and if stocking could be suppressing the productivity of some naturalized populations. Being one the world largest ecosystem manipulations, understanding the reproductive ecology of Chinook salmon in the Great Lakes is not only critical for the management of this introduced and sometimes contentious species (Crawford 2001; Claramunt et al. 2013), but can also provide a wealth of information on the naturalization process with implications for restoration of threatened, endangered, and extirpated wild fish populations.

2.5 References

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3 On the edge or down to the core? A comparison of commonly used methods for identifying juvenile habitat of fish using otolith microchemistry

3.1 Introduction

Otolith microchemistry has become a widespread technique in fish ecology and fisheries research. Otoliths are hard calcareous structures suspended in the fluid fill canals of the vestibular apparatus in the inner ear of teleost fish and function to aid fish with orientation (Secor et al. 1992). Otoliths continuously grow throughout the life of fish, primarily composed of calcium (Ca), oxygen (O), and carbon (C) (Campana, 1999). However, elemental impurities (microchemicals) reflective of the habitats in which fish reside can be chronologically incorporated into the otolith structure (Campana and Thorrold, 2001). Elemental impurities such as magnesium (Mg), strontium (Sr), and barium (Ba) may be substituted for calcium within the calcium carbonate crystal structure (Campana, 1999). These and other elemental impurities may also be captured in the interstitial spaces between the crystal structure, or associated with an organic matrix. By analyzing the microchemical concentrations, researchers are able to identify previously occupied habitats.

Otolith microchemistry has been used to study the timing of migration and the origins of migratory fish such as pike (*Esox lucius*) (Engstedt et al. 2010), North Atlantic cod (*Gadus morhua*) (Syedang et al. 2010), european eel (*Anguilla anguilla*) (Martin et al. 2010) and several salmonid species: Atlantic salmon, *Salmo salar* (Perrier et al. 2011); Chinook salmon, *Oncorhynchus tshawytscha* (Barnett-Johnson et al. 2010); rainbow trout, *Oncorhynchus mykiss* (Boehler et al. 2012). The technique has also been used to identify nursery habitat and spatial distributions in marine (Cook, 2011; Thorisson et al. 2011; DiFranco et al. 2012) and freshwater (Brazner et al. 2004a; Zeigler and Whitley 2011) fish populations. Otolith microchemical studies rely on the ability to consistently locate and microchemically analyse a section of otolith representing a particular life history stage (e.g., juvenile life history). The objective of this study was to test if four commonly published methods used for analysing juvenile otolith sections produce

different microchemical concentrations and have different performance in predicting juvenile habitat.

Studies using otolith microchemistry to identify juvenile habitat located and analysed the juvenile otolith section differently (e.g., DiFranco et al. 2012; Pangle et al. 2010; Tanner et al. 2012; Veinott and Porter 2013; Wolff et al. 2012). Study-specific concerns, such as fish species, otolith size and shape, sample size, as well as study objectives likely lead to differing methods among studies. Individual studies generally used one of four approaches: A) analysis of whole juvenile otoliths; B) analysis of otolith sections a standard distance from the core; C) analysis of a section at the edge of juvenile otoliths; and D) analysis of otolith sections based on microchemical signals associated with life history events. In otolith studies, the term “core” refers to various sections of the early life history growth region, including the point of nucleation (primordium) and up to the entire juvenile (age-0) growth section. For the purpose of this study, the term “core” will refer to the visually observed centre of the otolith. The term “primordium” or “primordia” will refer to the initial point(s) of nucleation identified by elevated manganese (Mn) concentrations (Melancon et al. 2008).

Method A analyses whole juvenile otoliths or the age-0 otolith region in older fish (e.g., adults). Some studies located and analysed this section based on visual location of microstructures (e.g., core and first annuli) (Ashford et al. 2011; Wolff et al. 2012). Other studies analysed a section that was a standard width from the core (Pangle et al. 2010; Clarke et al. 2010). Method A requires limited interpretation to locate the otolith section for microchemical analysis; however, the presence of a maternal signal that does not reflect juvenile habitat may be a potential source of error (Ruttenberg et al. 2005; Melancon et al. 2008). Studies using Method A and discriminant function analysis (DFA) reported classification accuracies to juvenile habitats that ranged from 53% (Cook, 2011) to 100% (Zitek et al. 2010).

To remove potential error associated with a maternal signal, Method B analyses a section of otolith starting a standard distance from the core. Some studies located and analysed this section based on visual inspection of microstructures (Barnett-Johnson et al. 2010; Martin et al. 2010; DiFranco et al. 2012), while other studies used a constant distance from the core (200 μm , Perrier et al. 2011). The width of the analysed section is

commonly standardized within a study; for example, Perrier et al. (2011) analysed a 400 μm section in Atlantic salmon and Barnett-Johnson et al. (2010) analysed a 500 μm section in Chinook salmon. Similar to Method A, Method B requires minimal interpretation when locating the section for microchemical analysis. Studies using Method B reported classification accuracies that ranged from 42% (Martin et al. 2011) to 91% (Perrier et al. 2011).

Method C analyses an otolith section of standard width from the juvenile otolith edge (e.g., Ferguson et al. 2011; Hayden et al. 2011; Boehler et al. 2012; Tanner et al. 2012; Zeigler and Whitley, 2010, 2011). The edge of the juvenile otolith would be representative of habitat occupied immediately prior to a fish being captured. Compared to the other methods, Method C requires the least amount of interpretation when locating the section for microchemical analysis. However, the practical use of Method C is limited because it cannot be directly applied to older fish (e.g., adults) for identification of juvenile habitat. Studies using Method C reported classification accuracies that ranged from 73% (Tanner et al. 2012) to 96% (Ferguson et al. 2011).

Method D analyses an otolith section based on life history events that are captured within the microchemistry, including shifts in Mn, Magnesium (Mg), Zinc (Zn), Barium (Ba) or Strontium (Sr) concentrations (Engstedt et al. 2010; Cook, 2011; Marklevitz et al. 2011; Standish et al. 2011). Shifts in Mn, Mg and Ba concentrations are associated with the boundary between the pre-hatch/maternal and early juvenile life histories (Ruttenberg et al. 2005). In salmonids, increases in Zn and Sr concentrations in the juvenile region of the otolith are associated with the onset of freshwater feeding (Arai et al. 2007). Method D requires careful interpretation of microchemical concentrations in the early-growth region of otoliths when locating the section for microchemical analysis. Studies using Method D reported classification accuracies that ranged from 52% (Standish et al. 2011) to 93% (Veinott and Porter, 2013).

There are qualitative advantages for each of the four methods for locating and microchemically analysing juvenile otolith sections; however, the wide range of reported accuracies of assignments to juvenile habitat provides little insight into which method is superior. The objective of this study was to quantitatively compare Methods A-D using a common dataset. Applying each method to a common dataset enables comparison of

accuracies, and other performance indicators. First, consistent preparation and analysis can be complicated by differences in growth rates, shape, and size in the three-dimensional structure of otoliths (Secor et al. 1992; Smith et al. 2006; Gaglinao and McCormich, 2009; Boehler et al. 2012). This complication affects otolith studies because there are logistical and financial trade-offs in the time to prepare and analyse each otolith sample and the total sample sizes of the study. Thus, a method accurately applied in higher frequency (%) to the common dataset would be superior to methods applied in lower frequencies. Second, site-specific otolith microchemical signals have previously been shown to vary temporally with the potential to decrease the accuracy of assignments to juvenile habitats (Pangle et al. 2011; Tanner et al. 2012). Thus, methods that produce temporally stable microchemical signals would be superior to methods that do not.

The quantitative comparison of Methods A-D in this study used a two stage approach. First, the statistical significance of differences in nine trace element concentrations: Mg, potassium (K), Mn, iron (Fe), Zn, rubidium (Rb), Sr, Ba and lead (Pb), produced by each method were tested. Second, the performance of each method applied to a common dataset was evaluated using three metrics: 1) the ability to assign fish to juvenile habitat; 2) the frequency of application to the common dataset (hereafter referred to as applicability); and 3) the ability to produce temporally stable trace element concentrations.

3.2 Methods

3.2.1 Sample collection, otolith preparation, and LA-ICP-MS analysis

Otoliths used in this study originated from the Marklevitz et al. (2011) study. Age-0 Chinook salmon ($n = 467$) were collected from 17 rivers and seven hatcheries in Lake Huron in 2007 and 2008. Otoliths were divided into a training dataset ($n = 361$) and a test dataset ($n = 106$). The training dataset contained fish from all 24 collection sites ($n = 14 - 16$ per collection site). If a site was sampled multiple times, only otoliths from the last collection in May 2007 were included in the training dataset. The test dataset contained all other otoliths from collection sites that were sampled multiple times. Sagittal otoliths were removed from fish, polished using 3M™ lapping film and analysed on the laser ablation inductively couple mass spectrometer (LA-ICP-MS) at the Great Lakes Institute

for Environmental Research (University of Windsor). Life history transects were ablated using a 20 μm ($\pm 2 \mu\text{m}$) wide laser beam. Targeting a primordium, transects ran through the centre of the core and off the otolith edge. Life history transects were ideally located in the posterior-dorsal quadrant (Secor et al. 1992). Transects were alternatively located in the posterior ventral quadrant if the posterior-dorsal quadrant was damaged or contained vaterite deposits. For specific details on collection, preparation and LA-ICP-MS analysis refer to Marklevitz et al. (2011).

3.2.2 Otolith analysis methods

Analyses of otolith sections within the life history transect and ICP-MS data integration were performed using Thermo Scientific Plasmalab software. For Method A, a section was analysed from a primordium to the otolith edge. A primordium was identified by a visual inspection with a corresponding Mn peak ($> 3\times$ the surrounding Mn signal) in the life history transect (Ruttenberg et al. 2005; Melancon et al. 2008). The edge of the otolith was determined by a tin (Sn) signal above the reference gas blank indicating the laser ablated the embedding epoxy. For Method B, a 50- μm section of otolith originating 250 μm from a primordium was analysed; if the otolith was less than 300 μm , a section 250 μm from a primordium to the otolith edge was analysed. For Method C, a 50- μm -wide section from the otolith edge was analysed. For Method D, a section starting at the apex of the first rise in Zn or Sr concentrations ($> 3\times$ surrounding core signal) was analyzed, moving along the life history transect from core to otolith edge.

Ablated transects without distinguishable primordia signals (Mn peaks) were not analysed for Methods A and B because the accurate and precise location of a primordium in the three dimensional matrix of the otolith could not be determined (Boehler et al. 2012). Any section with a Sn signal above the reference gas blank indicated the laser had burnt through the otolith material and into the embedding epoxy. These sections were excluded from further analysis.

3.2.3 Statistical analyses

3.2.3.1 Trace element concentrations comparison among methods

SAS® (version 9.2) statistical software package was used for all statistical analyses. Three-level Hierarchical Mixed Linear Models (HMLMs) were used to test significant differences of each of the nine trace element concentrations (Mg, K, Mn, Fe, Zn, Rb, Sr, Ba and Pb) among Methods A-D. These elements were selected by Marklevitz et al (2011) because research suggested they would be good predictors of natal streams in the Lake Huron region (Ludsin et al, 2006b) especially in salmonids (Melancon et al. 2005). The precision for all evaluated elements was within the < 10% coefficient of variation criteria outlined by Ludsin et al. (2006a) based on analysis of a National Institute of Standards and Technology, standard reference material 610 (trace elements in glass) (Marklevitz et al. 2011).

Using HMLMs enabled comparisons of trace element concentrations between methods while controlling for differences among collection sites and individual fish. For HMLMs, all nine trace element concentrations were log transformed to improve normality and homoscedasticity. Models were developed using the approach outlined by Singer (1998) with a covariance structure selected to minimize Akaike Information Criterion (AIC) (Littell et al. 1996). Using the PROC MIXED function, Method A, B, C or D was used as a level one fixed effect variable. The second and third level random effect variables were individual fish nested within collection site and collection sites, respectively.

3.2.3.2 Performance assessment

Linear discriminant function analysis (LDFA) followed methods outlined in Marklevitz et al. (2011). The concentrations of the nine trace elements were treated independently for each method. Log transformations were performed on six trace element concentrations (Mg, Mn, Zn, Sr, Ba and Pb) to improve data normality for all methods. Two trace elements (K and Rb) were log transformed for Method B, C and D. A backwards stepwise approach was used to select the trace element (Mg, K, Mn, Fe, Zn, Rb, Sr, Ba and Pb) to include in LDFA model for each method. The prior probabilities of

assignment (priors) to each site were proportional to the number of fish in each collection site for all models (Tabachnick and Fidell, 2007). The optimum LDFA model was selected independently for each method based on highest assignment accuracy (%).

A 1,000-iteration bootstrap resampling procedure was performed to calculate 95% confidence intervals and test differences in assignment accuracies among methods. During each iteration, 15 fish within each collection site in the training dataset were randomly sampled with replacement using SAS® randomization macro. Fish in the test dataset were not re-sampled. Assignment accuracies from jackknife classification of the training dataset and test data were calculated. Jackknife classification assigns group membership of each individual using functions derived from all other individuals in an iterative process until all individuals are assigned to a group. Biases of the LDFA models were defined as the difference between the original LDFA assignment accuracy and average assignment calculated from the resampling procedure (Efron and Gong, 1983; Jackson, 1986). Overlapping 95% confidence intervals indicated no statistical difference in assignment accuracy.

In addition to overall assignment accuracy (% of fish correctly assigned to juvenile habitat), site-specific assignments (% of fish assigned to each juvenile habitat) were examined for each fish. Assignments of individual fish to collection sites were pooled into four categories: 1) correctly assigned; 2) misassigned to a collection site within the same geological region; 3) misassigned to a collection site within close geographical proximity (outside of the geological region but within 150 km); or 4) misassigned to some other collection site. For further details on the criteria for these categories refer to Marklevitz et al. (2011).

The applicability of the methods were evaluated by examining the proportion (%) of otolith samples that met the criteria outlined in the “Otolith analysis methods” section for analysing the juvenile section of the life history transect.

The temporal variability of trace elements among collection dates within each method were tested using MANOVAs. The trace element concentrations (ppm) were transformed as outlined in the “Discriminatory performance” section. Comparisons were made using fish collected on several dates in 2007 (May 2, 17, 30, June 12) and 2008 (May 29) from the Sydenham River (Owen Sound, Ontario) (see Table 1 in Marklevitz et

al. 2011). Significant MANOVAs were followed with univariate ANOVAs to test differences in individual trace element concentrations.

3.3 Results

Methods A - D produced different ($p < 0.05$) concentrations of Mg, K, Mn, Zn, Rb, Sr and Ba (Table 3.1). Method A produced the highest Mg and Ba concentrations and had six of nine microchemical concentrations (Mg, K, Zn, Rb, Sr, and Ba) that differed from all other methods. Method B produced the lowest Mg concentrations. Method C produced the highest Mn concentrations. Method D had the fewest (2 of 9) trace element concentrations that were significantly different to the other methods.

The trace elements used in the LDFA models for Methods A and B excluded Pb, but excluded no trace element in Methods C and D. For all four methods, the majority of variability was explained by the first three discriminant functions: Method A = 88%, Method B = 84%, Method C = 85%, and Method D = 85%. All four methods had similar standardized loadings for the first three discriminant functions, identifying Sr, Fe, Ba and Zn (order of importance) as key trace elements for site-specific assignments.

Fish were assigned to juvenile habitat using all four methods (Table 3.2). The LDFA assignment accuracies of Methods A - D ranged from 73 - 85% for jackknife classified fish in the training dataset and 42% - 59% for fish in the test dataset (Table 3.2). There was no significant difference in site-specific assignment accuracy among methods for jackknife classified or test dataset results (Figure 3.1). Assignment accuracy from the test dataset was significantly lower than the jackknife classified results from the training dataset for all methods. The LDFA models had a bias tendency to underestimate assignment accuracy (0% - 4%) of jackknife classified site assignments. Assignment accuracy of the test dataset were underestimated by the LDFA models for Methods A (1%) and D (3%), but were overestimated for Methods B (3%) and C (1%). Common misassignments occurred when fish were assigned to another collection site within the same geological region. Ninety-three to 96% of the fish in the training dataset and 71% - 88% of fish in the test dataset were correctly assigned or assigned to another site within the same geological region. The second common misassignment occurred when fish were assigned to another site within geographical proximity (< 150 km) but in an adjacent

geological region (Table 3.2). Ninety-seven to 99% of fish in the training dataset and 94% - 100% were correctly assigned, fish assigned to sites within the same geological region or sites outside of the geological region but within geographical proximity (< 150 km).

Methods A - D could not be applied with equal frequency to the common dataset using the strict criteria for analysing the otolith sections specific in the methods section. Method A could be applied to 54% and Method B to 58% of the 467 otoliths. Method C was applied to 98% and Method D to 96% of the otoliths (Table 3.2).

No method produced temporally stable trace element concentrations among fish collected in the Sydenham River. Otolith microchemistry differed significantly within each method across collection dates – Method A: MANOVA, Wilks $\lambda= 0.00003$ F36, 106.67 = 43.08, $p < 0.0001$; Method B: MANOVA, Wilks $\lambda= 0.00018$ F36, 132.9 = 33.26, $p < 0.0001$; Method C: MANOVA, Wilks $\lambda= 0.00080$ F36, 234.08 = 37.16, $p < 0.0001$; and Method D: MANOVA, Wilks $\lambda= 0.00023$ F36, 234.08 = 54.66, $p < 0.0001$. With the exception of Mn for Method A and Pb for Method B, ANOVAs showed significant differences in the trace element concentrations within each method among collection dates (Table 3.3).

Table 3.1: Summary of hierarchical mixed linear models (HMLMs) comparing trace element concentrations produced by Methods A-D. Estimates for the random effects (Z statistic) of collection site (b_c) and individual nested within collection site ($b_{i(c)}$) are presented. Statistics for among method comparison, F statistic and pairwise comparisons (indicated with superscripts) were performed on log transformed data, but predicted mean trace element concentrations controlling for individual nested within sample site are presented. Superscripts (A, B, C, and D) indicate methods with similar trace element concentrations; the lack of superscripts indicates statistical difference.

Trace element	Collection site b_c est, $Z_{23,328}$	Individual (collection site) $b_{i(c)}$ est, $Z_{3,668}$	Method Predicted means (ppm)				
			$F_{3,69}$	A	B	C	D
Mg	0.229, 3.30*	0.063, 8.32**	29.88**	50.8	26.2	38.2	32.5
K	0.014, 3.26*	0.008, 11.64**	14.08**	1823	1702 ^D	1749 ^D	1727 ^{B, C}
Mn	0.046, 3.12*	0.039, 8.33 **	63.33**	5.09 ^D	3.16	7.23	4.94 ^A
Fe	0.286, 3.34*	0.053, 10.20**	0.91	316.9 ^{B, C, D}	323.1 ^{A, C, D}	334.8 ^{A, B, D}	319.0 ^{A, B, C}
Zn	0.021, 3.34*	0.003, 8.39**	397.24**	170.2	239.3	276.7	252.9
Rb	0.012, 3.22*	0.008, 10.18**	30.98**	0.19	0.38 ^D	0.33	0.37 ^B
Sr	0.111, 3.38*	0.004, 9.08 **	48.19**	452.9	521.4 ^D	540.3 ^D	527.2 ^{B, C}
Ba	0.079, 3.37*	0.006, 8.42**	10.20**	7.15	6.38 ^{C, D}	6.25 ^{B, D}	6.29 ^{B, C}
Pb	0.0003, 2.91*	0.0006, 9.86**	0.80	0.030 ^{B, C, D}	0.027 ^{A, C, D}	0.033 ^{A, B, D}	0.030 ^{A, B, C}

* $p < 0.05$, ** $p < 0.0001$

Table 3.2: Summary of comparisons among Methods A - D for analysing juvenile otolith sections. Average section widths and distances from core are reported \pm one standard deviation when applicable. The number (n) of applicable samples for each method in the training and test datasets are reported. Linear discriminant function analysis (LDFA) performance is presented as the percentage of site-specific assignments of individual fish: correctly assigned to juvenile site, assigned to another collection site within the same geological region (within), assigned to a collection site in an adjacent geological region within geographical proximity (< 150 km separation) (adjacent), or assigned to a collection site in a different geological region not in geographical proximity (different).

Method (description)	section width (μm)	distance from core (μm)	n		LDFA Performance (%)							
					Training				test			
					correct	within	adjacent	different	correct	within	adjacent	different
A) whole otolith (core to edge)	363 ± 102	0	194	58	0.91	0.05	0.04	0.01	0.29	0.59	0.12	0.00
B) standard distance from core (250-50 μm from core)	46 ± 11 max 50	250	200	65	0.83	0.12	0.05	0.01	0.29	0.42	0.23	0.06
C) standard distance from edge (last 50 μm from edge)	50	477 ± 243	352	105	0.87	0.06	0.04	0.03	0.48	0.30	0.19	0.04
D) internal elemental signal (Zn or Sr apex to edge)	190 ± 119	334 ± 183	346	103	0.89	0.07	0.03	0.02	0.42	0.38	0.16	0.05

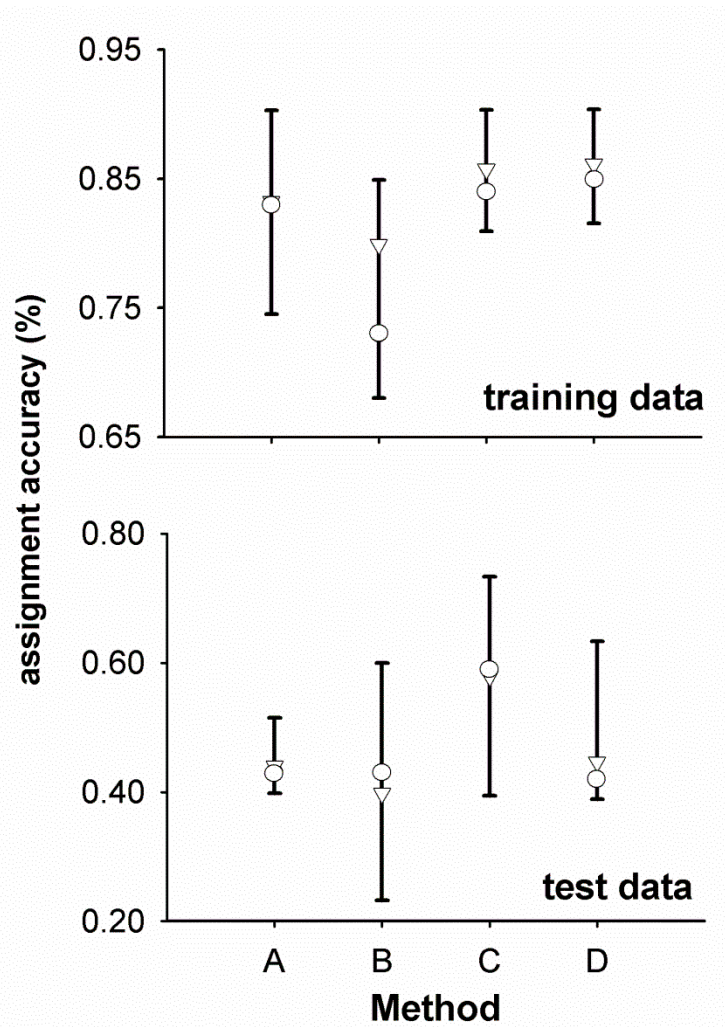


Figure 3.1: Linear discriminant function analysis (LDFA) assignment accuracy and bias comparison among Methods A - D. Jackknife classification of the training dataset and test data results are presented. Circles represent the assignment accuracy of the original LDFA model and triangles represent the mean assignment accuracy based on bootstrapped LDFA models. Differences between circles and triangles indicate bias in original LDFA classifications. Error bars represent 95% confidence intervals based on bootstrapped LDFA models, and overlapping bars indicate no statistical difference.

Table 3.3: Summary of temporal trace element concentration comparisons (ANOVAs) within each Method (A - D). Juvenile (age-0) Chinook salmon otoliths were collected 2, 17, and 30 May and 12 June, 2007 and 29 May, 2008 from the Sydenham River (Owen Sound, Ontario).

Trace element	Method			
	A	B	C	D
	F _{4,36}	F _{4,43}	F _{4,75}	F _{4,70}
Mg	10.37**	6.88*	13.68**	12.39**
K	31.71**	39.19**	37.01**	63.11**
Mn	1.89	25.56**	87.96**	65.20**
Fe	6139.6**	429.70**	112.84**	1522.93**
Zn	91.44**	44.21**	36.84**	103.15**
Rb	13.29**	46.30**	38.53**	53.32**
Sr	36.73**	38.23**	56.34**	75.85**
Ba	3.91*	3.93*	15.16**	13.63**
Pb	3.46*	1.28	2.62*	4.34*

* $p < 0.05$, ** $p < 0.001$

3.4 Discussion

Otolith microchemical analysis enables aquatic and marine ecologists and fisheries researchers to address many previously unanswered questions such as natal origins and habitat use of fish populations and stock structure of fisheries. The use of microchemistry has increased from around two publications $\cdot \text{yr}^{-1}$ in the early 2000s to >19 publications $\cdot \text{yr}^{-1}$ since 2010 (based on Web of Science indexed articles, search criteria, topic = “otolith” and “*chemistry” and “origin*”). Otolith microchemical studies have also increased in scope and size. For example, Brazner et al. (2004a) examined juvenile origins and connectivity between coastal wetlands using 64 Yellow perch (*Perca flavescens*) otoliths from four sites (within 40 km) in Lake Superior. Cook (2011) examined dispersal rates of damselfish (*Garibaldi Hypsypops rubicundus*) using 1,101 larval and 72 juvenile otoliths from six reefs (within 60 km) along the California coast. As the application of otolith microchemical analysis has expanded, increasing attention has been placed on testing assumptions and the limitations of the technique. Some researchers focused on the statistical methods used to assign juvenile origins in efforts to increase accuracy and produce robust conclusions (Munch and Clarke, 2008; Mercier et al. 2011). Other researchers focused on microchemical analysis considerations such as temporal stability of trace element concentrations (Pangle et al. 2010; Tanner et al. 2011; Reis-Santos et al. 2012) or analytical methods such as depth of ablated transect (Hooper and Jones, 2013). My study showed how four common methods for locating and analysing the juvenile otolith sections produced different trace element signatures but assigned fish to similar juvenile habitats. The differences in trace element concentrations but similarities in juvenile habitat assignments demonstrated that consistently analysing a section of otolith was more important than the method used when assigning the location of juvenile origin (Table 3.4).

Table 3.4: Summary of strengths and weaknesses of different published methods for analysing the microchemistry of juvenile otolith sections.

Method (description)	Excludes maternal signal: (a potential source of error)	Accuracy:		Susceptible to		Applicable to adult otoliths
		reported in literature	to common dataset	inaccuracy in otolith preparation and analysis	temporal variability in microchemical signal	
A) whole otolith (core to edge)	No	53% - 100%	91%	Yes	Yes	Yes
B) standard distance from core (250-50 μ m from core)	Yes	42% - 91%	83%	Yes	Yes	Yes
C) standard distance from edge (last 50 μ m from edge)	Maybe	73% - 96%	87%	No	Yes	No
D) internal elemental signal (Zn or Sr apex to edge)	Yes	53% - 93%	89%	potentially compensates	Yes	Yes

Method A (whole juvenile otolith including the primordium) had the highest number of trace element concentrations (six of nine trace elements) that differed from the other methods. This method produced the highest concentrations of Mg and Ba, which is consistent with previous studies that found elevated Mg and Ba concentrations in otolith cores or primordia compared to the surrounding material (Ruttenberg et al. 2005; Melancon et al. 2008). Ruttenberg et al. (2005) and Melancon et al. (2008) also found elevated Mn concentrations in the otolith cores or primordia. While Method A produced higher Mn concentrations than Methods B and D, the highest concentrations were produced by Method C (edge section). During examination of the life history transects, increasing Mn concentrations were observed near the edge of otoliths, approximately 350 to 600 μm from a primordium. The cause of increased Mn concentrations at the edge of age-0 Chinook salmon is unknown. Concentrations of Mn in otoliths differ among aquatic habitats and display seasonal cycles in aquatic environments with the highest concentrations in summer (Brazner et al. 2004b; Elsdon and Gillanders, 2006; Halden and Friedrich, 2008). The increase in Mn concentrations at the edge of the age-0 Chinook salmon may reflect changes in feeding, metabolism of fish or the formation of the crystal structure of calcium carbonate otolith (Melancon et al. 2005; Arai et al. 2007). Methods B (juvenile otolith excluding the maternal signal) and D (freshwater feeding section) commonly analysed similar sections of the life history transect and had the fewest differences in trace element concentrations (three of nine trace elements). The highest concentrations of Sr were produced by Methods B and D, consistent with the onset of the freshwater feeding in salmonids (Arai et al. 2007).

Despite differences in trace element concentrations, all methods produced analogous LDFA models. There were similar discriminant function loading factors on trace element concentrations (i.e., key trace element Sr, Fe, Ba and Zn) among all methods. The discriminatory performance, frequency of correct assignments and nature of misassignments were also similar among all four methods. Fish were commonly misassigned to a site in the same geological region or within geographical proximity (< 150 km). These results are consistent with geologic, anthropogenic and atmospheric sources of trace elements in aquatic environments (Campana, 1999; Marklevitz et al. 2011).

The ability to consistently analyse the section among all otoliths in the common dataset varied from 54 to 98% among the methods. The minor differences in applicability (< 10%) among methods resulted from sample loss when the laser burnt through the otolith into the embedding epoxy. Major differences in applicability were between methods that were dependent (Methods A and B) and independent (Methods C and D) of the inclusion of a primordium within the life history transect. In the present study, visual location of cores together with a primordium microchemical signal (Mn peak) for Methods A and B was considered a stringent criterion. Previous studies commonly only visually locate cores (e.g., Barnett-Johnson et al. 2010; Martin et al. 2010; DiFranco et al. 2012; Macdonald et al. 2013). Visually locating the core treats otoliths as two-dimensional structures, ignoring the complexities of the three dimensional shape and growth (Hoover and Jones, 2013). Because of an otolith's three-dimensional translucent structure, visually locating an ablated transect through a core leaves the potential that a transect is located above or below the plane of growth, the anatomical plane containing all growth increments including a primordium (Secor et al. 1992; Boehler et al. 2012). When ablated transects are not in the plane of growth, Method A would analyse varying and unquantifiable amounts of material in the core region (i.e., maternal signal), and standardized measurements used in Method B would not be made from a standard point in the otolith. As my study illustrates, analysing different otolith sections will produce different trace element concentrations. Hoover and Jones (2013) also found the depth that a laser ablates into an otolith structure will affect otolith trace element concentrations. More consideration of the three-dimensional structure of otoliths is needed in future otolith microchemical analysis.

None of the methods used to analyse the juvenile section of the otolith produced temporally stable trace element concentrations. Ultimately, otolith microchemistry results from complex interactions among environmental chemistry (concentrations, temperature and pH), physiology of fish and calcium carbonate mineralization of the otolith structure (Kalish, 1989, 1991; Elsdon and Gillanders, 2006; Melancon et al. 2009). Pangle et al. (2011) and Tanner et al. (2011) showed that site-specific microchemistry differed significantly within and between years. Temporally unstable site-specific microchemistry would explain the lower site-specific assignment accuracies of the test dataset when

compared to the training dataset (Figure 3.1). However, temporally unstable microchemistry does not always reduce the ability to accurately assign fish to juvenile habitats (Tanner et al. 2011). In the test dataset, site-specific accuracy declined, but 94% - 100% of fish were still assigned to juvenile rivers or hatcheries within the same geological region or within geographical proximity. To incorporate temporal variability into otolith microchemical analysis, Pangle et al. (2010) suggested that site-specific “libraries” of microchemical signals be developed over the timeframe of interest for a given study. These temporally unstable microchemical signals are inherent and should be addressed during study design in future research.

The findings of my study have three important implications for future otolith microchemical studies. First, when using otolith microchemistry to assign juvenile habitats it does not matter how the juvenile section of otolith is located; however, it is crucial that there be consistent analysis of the section in all otoliths within a study. Second, when analysing otolith sections, the three dimensional structure of the otolith must be taken into consideration. Third, temporal instability of otolith microchemistry cannot be addressed or corrected during microchemical analysis and must be considered during study design. Combined with studies such as Munch and Clarke (2008), Pangle et al. (2010), Mercier et al. (2011), Tanner et al. (2011) and Hooper and Jones (2013), the present study adds to the growing body of literature testing the assumptions and limits of otolith microchemistry analysis to improve the accuracy and robustness of conclusions.

3.5 References

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4 Otolith microchemistry reveals spatio-temporal incomplete mixing of fish from natal sources and inter-basin migrations of Chinook salmon in Lake Huron

4.1 Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) were introduced into the Laurentian Great Lakes to convert nuisance levels of invasive alewife (*Alosa pseudoharengus*) into recreational fishing opportunities (Kocik and Jones, 1999). Since the late 1960s, intensive stocking programs have maintained the abundance of Chinook salmon throughout several Great Lakes, but naturalized (wild) populations have become established (Crawford, 2001; Claramunt et al. 2013). Since the early 2000s, naturalized fish have been contributing over 80% of the Chinook salmon harvested by the Lake Huron recreational fishery (Johnson et al. 2010; Claramunt et al. 2013). Despite the prevalence of naturalized Chinook salmon in Lake Huron, coordinated lake wide research and monitoring of this species has been limited. The lack of information about Chinook salmon limits our understanding of their basic ecology, including how different hatcheries or naturalized populations contribute to the fishery. The objective of this study was to use otolith microchemistry to identify natal sources of Chinook salmon in Lake Huron and test the common assumption of a completely mixed-stock fishery.

Naturalized populations of Chinook salmon were first discovered in Lake Huron during the 1980s in several Southern Georgian Bay rivers and shoal spawning was reported in the North Channel (Carl, 1982; Kerr and Perron, 1986; Kerr, 1987; Powell and Miller, 1990). More recently, naturalized populations have been documented in 17 rivers; however, the sizes of these populations and their contributions to the lake wide fishery are unknown (Johnson et al. 2010; Marklevitz et al. 2011). Hatchery supplementation has continued despite the establishment of naturalized populations. Hatchery programs collect gametes annually from hatchery and naturalized origin fish

returning to collection weirs. From 1968 to 2010, 111 million Chinook salmon were reared in hatcheries and stocked into the lake, with the majority released along the Michigan coast (FWS/GLFC, 2010). The fishery is therefore composed of fish with different juvenile-rearing histories (hatchery versus naturalized) originating from different natal locations.

Understanding the spatial and temporal variability in stock composition is basic information about population ecology critical for proper fisheries management. Spatio-temporal variation in biotic and abiotic conditions can affect the growth, body condition, age at maturation, and survival of Chinook salmon (Wells et al. 2006, 2007, 2008, 2012). In Lake Huron, interactions between prey availability and Chinook salmon density could influence intraspecific competition or interspecific competition with native lake trout (*Salvelinus namaycush*) (Riley et al. 2008; Roseman and Riley, 2009). With multi-agency management of the fishery, there are differing intensities of stocking and fishing pressure throughout the lake (Claramunt et al. 2013). For example, while Chinook salmon are predominately targeted by anglers in a multimillion dollar recreational fishery, in northern US waters they are also targeted in a small commercial gill net fishery. Furthermore, the intensity of the recreational fishery is a function of access to the fishing grounds and proximity to population centers. Some areas of Lake Huron have almost no access sites, especially in Ontario. Migration of Chinook salmon throughout the lake therefore exposes fish to different factors that can influence growth and survival rates among populations. To date, lack of information has forced fisheries management agencies of Lake Huron to make some general assumptions of stock composition including: a completely mixed fishery; lack of immigration or emigration from the Main Basin to other basins (i.e., Lake Michigan and Georgian Bay); constant age-specific selectivity and natural mortality rates; and survival rates independent of rearing origin (Adlerstein et al. 2007; Brenden et al. 2012).

In their native range, Chinook salmon migrate thousands of kilometres from natal rivers to foraging areas in the ocean before returning to natal rivers to spawn (Quinn, 2005). Populations from similar geographic regions have similar oceanic distributions, which appear to be consistent over time (Weitkamp, 2010). In foraging areas at sea, populations of varying sizes co-mingle to form “mixed stock fisheries”. Chinook salmon

remain in mixed stock fisheries for 2 to 3 years before homing back to natal rivers (Dittman and Quinn, 1996; Quinn, 2005). The spatial precision of natal homing by Chinook salmon is extraordinary. One study showed over 99% of fish surviving to maturity returning to their natal river system (i.e., Columbia River system) with > 98% returning to their precise natal river (e.g. Cowlitz River) (Quinn and Fresh, 1984). Beyond some basic knowledge of oceanic distributions, much of the at-sea ecology of Chinook salmon remains unknown. Logistical challenges also mean most of our knowledge about the at-sea salmonid ecology is derived from marked hatchery fish recaptured in fisheries (Quinn, 2005; Weitkamp, 2010; Quinn et al. 2011).

Similar to Chinook salmon in their native range, most of our ecological knowledge of Chinook salmon in Lake Huron is based on mark-recapture studies of hatchery fish. For example, comparing capture rates of marked to unmarked fish revealed increasing captures of presumably naturalized fish from 15% of the fishery in 1991 - 1995 to >80% in 2000 - 2010 (Adlerstein et al. 2007; Johnson et al. 2010; Brenden et al. 2012). Recaptures of Michigan-stocked fish also revealed long-distance movements by Chinook salmon within the Main Basin of Lake Huron (Adlerstein et al. 2007). Recaptures primarily along the Michigan Coast suggest Chinook salmon move northwards from May to July and southwards from August to October, when some presumably return to natal rivers or stocking sites to spawn. These extensive movements support the assumption that the Chinook salmon fishery in Lake Huron is a single management unit or stock (Adlerstein et al. 2007). On the other hand, spatial variability in the percentage of naturalized fish suggests otherwise (Johnson et al. 2010).

Basing our ecological knowledge of Chinook salmon in Lake Huron on hatchery fish has two major limitations. First, the majority of research and monitoring occurs along the Michigan coast which is also where the majority of stocking occurs (e.g. Diana, 1990; Adlerstein et al. 2007; Johnson et al. 2007; Bence et al. 2008). This means that the eastern coast of the Main Basin, the North Channel, and Georgian Bay where the majority of naturalized populations are located, has been excluded from most research and monitoring programs (Marklevitz et al. 2011). Second, hatchery rearing and stocking locations may influence migration routes and timing via non-adaptive phenotypic plasticity. Timing of juvenile out-emigration from rivers, homing rates and arrival timing

of adults to spawning sites, and spatial distributions of spawning fish often differ between hatchery and wild fish (Daugherty et al. 2003; Hoffnagle et al. 2008; Dittman et al. 2010). While mass marking of naturalized Chinook salmon to study movements and distributions within Lake Huron is possible, such studies pose significant financial and logistical challenges.

Analysis of population-specific markers can reduce the dependence on mass marking to identify origins of fish. Microsatellite DNA variation is one type of natural marker used to identify natal locations of salmonids (Seeb et al. 2004; Beacham et al. 2008; Tucker et al. 2009). However, microsatellite analysis of Chinook salmon in Lake Huron would be minimally useful because of limited genetic divergence and an inability to differentiate among many of the naturalized populations (Suk et al. 2012). Otolith microchemistry has also been used to identify the natal locations of Chinook salmon (Barnett-Johnson et al. 2007, 2010; Brennan et al. 2015; Miller et al. 2010), including within the Great Lakes (Marklevitz et al. 2011). As otoliths grow, they permanently and chronologically incorporate major, minor and microchemical (trace element) impurities at environmentally-representative concentrations into the calcium carbonate structure (Campana, 1999; Campana and Thorrold, 2001). Not only can elements vary in their concentration, the isotopes of some elements can vary relative to other isotopes of the same element. For example, strontium and sulfur isotope ratios have been used to discriminate marine versus freshwater environments or diets in salmonid fishes (e.g., Kennedy et al. 2000, Weber et al. 2002; Bacon et al. 2004). Strontium isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$) are also known to vary with geological features and can be used to delineate natal origins (Wadleigh et al. 1985; Hodell et al. 1989; Brennan et al. 2015). Therefore, the natal source of adult fish should be predictable by comparing the microchemistry (i.e., elemental concentrations and $^{87}\text{Sr}/^{86}\text{Sr}$ isotopic ratios) in the juvenile section of adult otoliths to otoliths from juveniles collected from known natal sources.

The objective of this study was to use otolith microchemistry to identify natal sources of Chinook salmon captured throughout the Lake Huron fishery. Within the Lake Huron watershed, juvenile salmon occupy rivers in regions with different bedrock and surficial geology. Previous research found, this led to highly structured variation in multi-element concentrations in the otoliths of juveniles caught in natal rivers and hatcheries, and to the

ability to classify natal sources based on otolith microchemistry with high (87%) accuracy (Marklevitz et al. 2011). The presence of some natal sources on the Canadian Shield means that analyses of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in juveniles and adults could help further discriminate fish from this Precambrian geological region, and regions containing younger surficial geology (Hodell et al. 1989; Bacon et al. 2004). In this study, otoliths were collected from adult Chinook salmon sampled opportunistically from Lake Huron recreational fisheries in 2008 and 2010. Natal sources were identified based on otolith microchemistry comprising both multi-element concentrations and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios, and evaluated the contributions of different hatcheries and naturalized populations to the lake wide fishery. By identifying the natal source of individuals, the spatial and temporal variability in sample composition were examined to assess the assumption of a completely mixed fishery.

4.2 Methods

4.2.1 Sample Collection

In 2008 and 2010, adult Chinook salmon were collected through established Lake Huron fisheries assessment programs. Sampling was performed by Western University (Canada), Ontario Ministry of Natural Resources and Forestry (OMNRF), and Michigan Department of Natural Resources personnel. Although attempts were made to stratify collections of fish from the lake through space and time, only opportunistic sampling of the in-lake fishery was accomplished. The majority ($n = 464$) of fish were solicited from anglers through recreational angler (creel) survey and at fishing derby weigh stations. A few additional fish ($n = 17$) were sampled as by-catch in commercial fisheries. To validate natal source assignments of adult fish, fish were also collected as they returned to spawn in the Sydenham and Beaver Rivers, which flow into Southern Georgian Bay. The Sydenham River was sampled in 2007 ($n = 19$) and 2010 ($n = 35$). The Beaver River was sampled in 2010 ($n = 11$). The presence or absence of an adipose fin clip was noted for all fish. Whereas Ontario (Canadian) hatcheries exclusively marked stocked fish using adipose fin clips, Michigan (US) hatcheries marked with combinations of oxytetracycline dye (OTC) and adipose fin clips. However, Michigan hatchery fish were not marked in 2004 or 2005, which represent age-4 and age-3 fish, respectively, in the 2008 fishery

(Johnson et al. 2010). A section of caudal vertebrae was sampled from each fish for OTC analysis according to Johnson et al. (2010). The sagittal otoliths were removed, cleaned of adhering tissues and stored dry in micro-centrifuge vials.

The capture locations of fish were recorded based on statistical districts used for fisheries management (see frontispiece map in Riley, 2013). Statistical districts of capture locations were pooled into four broad capture regions according to Table 4.1 and presented in Figure 4.1: Northern Huron (NH_c, the subscript denotes “capture”); Central Huron (CH_c); Southern Huron (SH_c); and Georgian Bay (GB_c). Capture dates were pooled into spring (S), early summer (ES) and late summer (LS). Spring (April-June) represents a period when previous studies assumed that Chinook salmon would be completely mixed throughout the lake (Adlerstein et al. 2007; Johnson et al. 2010). Early summer (July) represents a transition period when maturing fish would begin to aggregate in preparation for their spawning migrations (Quinn, 2005). Late summer (August-November) represents a period when sexually-maturing fish are expected to undertake spawning migrations, resulting in maximum spatial heterogeneity in the fishery with respect to stock composition (Adlerstein et al. 2007; Kocik and Jones, 1999; Quinn, 2005).

4.2.2 Otolith analysis

Otoliths were thin sectioned by fish-aging specialists at the Northwest Science and Information Office of OMNRF. One sagittal otolith (right or left) was selected at random for analysis, excluding any that were cracked, broken or contained significant amounts of vaterite deposits [see Secor et al. (1992) for definitions and descriptions of otolith terminology]. Otoliths containing vaterite were excluded because this crystal structure of calcium carbonate incorporates elements differently than the normal aragonite structure found in otoliths (Melancon et al. 2005). Otoliths were individually embedded, sulcus side down, in marine grade epoxy resin. A Buehler isomet saw was used to cut 0.5 mm sections perpendicular to the sulcus (transverse section) from the widest dorsal-ventral width of the otolith. To expose a clean smooth surface in the plane of growth, otolith sections were individually polished using sequentially finer grit lapping film (3M, www.3M.com).

Table 4.1: Summary of Chinook salmon sampled, by capture region, statistical district, and period from the Lake Huron recreational fishery in 2008 ($n = 79$) and 2010 ($n = 402$). Capture regions are shown in Figure 4.1 and statistical districts are fisheries management units presented in Riley (2013).

Year	Capture region	Statistical districts	Spring	Early summer	Late summer
2008	NH _c	MH1,2, OH1, NC1	15	8	22
	CH _c	OH3			
	SH _c	OH5	19		
	GB _c	GB4	15		
2010	NH _c	MH1,2, OH1, NC1	14	84	155
	CH _c	OH3		25	11
	SH _c	OH4, OH5	26		6
	GB _c	GB4			81

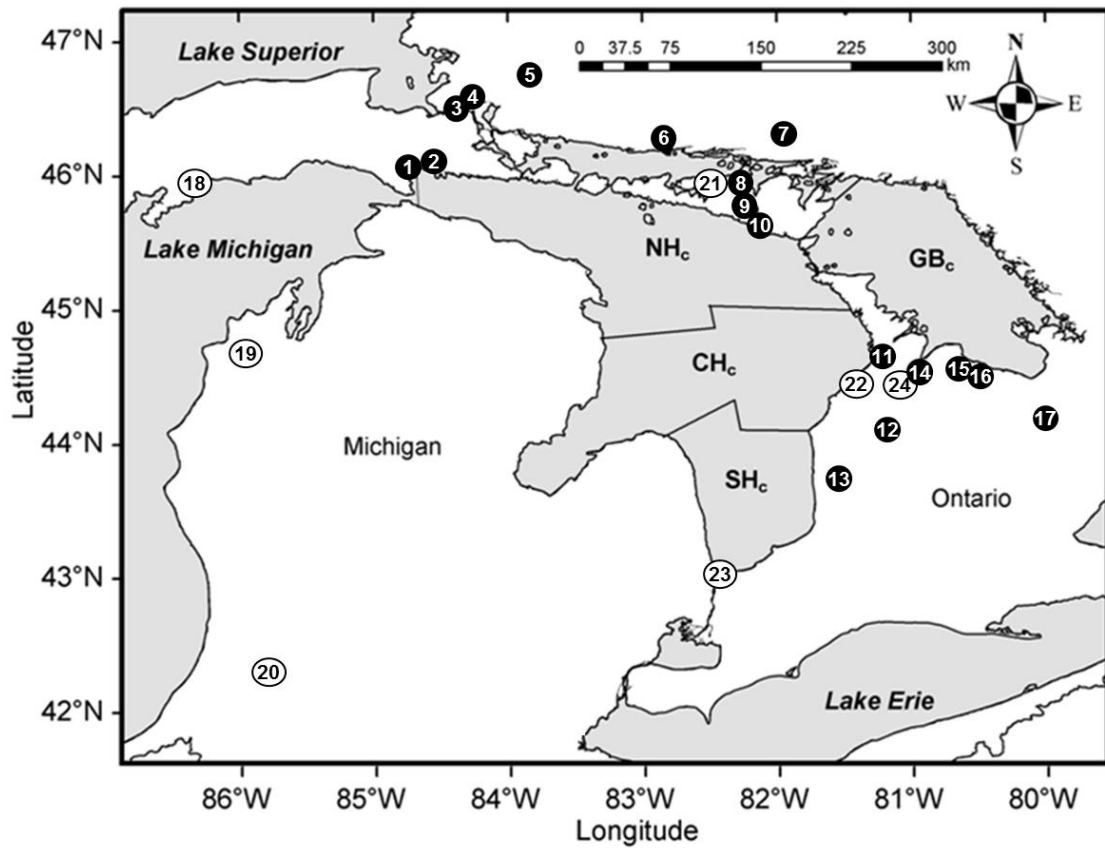


Figure 4.1: Map of Lake Huron showing the capture regions. Natal sources of Chinook salmon are indicated with closed numbered circles for naturalized populations and open numbered circles for hatcheries; numbers correspond to natal sources in Table 4.2. GB_c refers to Georgian Bay, NH_c refers to Northern Huron (Main Basin and North Channel), CH_c refers to Central Huron (Main Basin), and SH_c refers to Southern Huron (Main Basin).

Microchemical analysis was performed on otolith sections using a laser-ablation inductively-coupled plasma mass spectrometer (LA-ICP-MS) at the Great Lakes Institute for Environmental Research (University of Windsor, ON). A Quantronix Integra-C femto-second laser source produced a 785 nm laser beam, which was directed into an Olympus BX51 microscope to produce a final ablation pit diameter of 20 μm ($\pm 2 \mu\text{m}$). The laser ablated a transect parallel to the distal otolith edge passing through the centre of the core and the dorsal apex. This location was used to standardize transects and minimize variability among otoliths (Campana, 1992). The sulcus groove was used to visually locate the core region and the ICP-MS analysis time was noted as this section crossed the laser beam. Surface contaminants were removed by first passing the otolith under the laser traveling at 20x analytical speed (Christiansen, 2011). For LA-ICP-MS analysis, transects were re-ablated with otoliths traveling at 5 to 15 $\mu\text{m} \cdot \text{s}^{-1}$. Ablated otolith material was carried by argon gas to a Thermo Scientific X2 ICP-MS.

Thermo Scientific Plasmalab software was used to process multi-elemental data for 15 isotopes: magnesium (^{25}Mg), potassium (^{39}K), calcium (^{43}Ca and ^{44}Ca), manganese (^{55}Mn), iron (^{57}Fe), zinc (^{66}Zn and ^{67}Zn), rubidium (^{85}Rb), strontium (^{86}Sr and ^{88}Sr), tin (^{118}Sn and ^{120}Sn), barium (^{138}Ba) and lead (^{208}Pb). A 60 s gas blank was analyzed prior to each otolith for background subtraction. To correct for instrument drift and determine limits of detection, duplicate NIST 610 glass standards were ablated before and after every 8 to 17 otoliths. To correct for variation in the amount of ablated material, microchemical concentrations were standardized to an otolith Ca concentration of 400,432 ppm (pure CaCO_3). Adjustments for background subtraction, instrument drift, limits of detection and amount of ablated material were performed using a Microsoft Excel spreadsheet macro (Yang, 2003). Instrument precision for all measured elements was within the 10% coefficient of variation criteria outlined by Ludsin et al. (2006).

The juvenile sections of adult otolith transects were identified for analysis. Numerical integration was done to convert raw ICP-MS data ($\text{counts} \cdot \text{sec}^{-1}$) to elemental concentrations (ppm). In relation to the core centre, the juvenile section began at the first rise ($> 3x$ core signal) in the Zn or Sr signal and ended at shifts in the Sr, Zn and Mn signal located 350 to 600 μm from the core centre. A rise in Zn or Sr concentrations associated with the onset of exogenous feeding and the freshwater growth zone (200 to

800 μm from the core centre) of the otolith has previously been reported in salmonid otoliths (Araki et al. 2007). An elevation in Mn concentrations was observed at the edge of age-0 Chinook salmon otoliths (350 to 600 μm from the core centre) from Lake Huron rivers and hatcheries (Marklevitz et al. 2011). A shift in Sr, Ba, Mg and Mn concentrations, hypothesized to be associated with the transition from hatchery to lake environments, was also observed in the otoliths of hatchery steelhead trout (*Oncorhynchus mykiss*) in Lake Erie (Boehler et al. 2012).

In addition to estimating elemental concentrations in otoliths, I measured $^{87}\text{Sr}/^{86}\text{Sr}$ isotopic ratios for a subset of the adult Chinook salmon ($n = 102$). Isotopic analysis was performed with the same laser ablation system but coupled to a NEPTUNE multicollector ICP-MS. Because $^{87}\text{Sr}/^{86}\text{Sr}$ analysis was not included in Marklevitz et al. (2011), analysis was performed on a subset of juveniles ($n = 171$) from 12 of the 24 sites used in this prior study. Details of Sr isotopic analyses for otoliths and data acquisition and reduction protocols are in Yang et al. (2011).

4.2.3 Assignment of natal region

Mercier et al. (2011) proposed several parametric statistical and machine learning methods for use with otolith microchemistry to assign natal sources: linear discriminant function analysis (LDFA), quadratic discriminant function analysis, artificial neural networks, and random forest analysis. The LDFA of Chinook salmon juveniles developed by Marklevitz et al. (2011) was compared to the other methods. Using the R program from Mercier et al. (2011) and the model training dataset from Marklevitz et al. (2011), assignment accuracies to 24 collection sites (17 rivers and seven hatcheries; see Table 4.2) from the four methods were compared. Linear discriminant function analysis had higher mean assignment accuracy ($81 \pm \text{SD} = 4\%$) than quadratic discriminant function analysis ($64 \pm 5\%$) and artificial neural networks ($66 \pm 6\%$). Random forest analysis ($86 \pm 4\%$) had a slight improvement over LDFA analysis when using the Mercier et al. (2011) R program. The accuracy of random forest analysis using R was similar to the LDFA accuracy in Marklevitz et al. (2011) using SAS (87%). LDFA in SAS was used for consistency with Marklevitz et al. (2011) and because assignment accuracy was not

improved with the more complicated and less transparent random forest analysis (Mercier et al. 2011). SAS® (version 9.2) was used for all subsequent statistical analyses.

The natal sources (river or hatchery) of all adult Chinook salmon were predicted using the site-specific LDFA model from Marklevitz et al. (2011). LDFA is a multivariate method used to predict group membership based on a set of predictor variables. LDFA first derives classification functions for individuals with known group memberships. Model accuracy is assessed by jackknife classification, whereby each individual is classified using functions derived from all other individuals. Classification to group involves the comparison of posterior probabilities of assignment (p_{assign}) for each possible group with individuals assigned to the group with the maximum posterior probability of assignment ($\max\{p_{\text{assign}}\}$). These classification functions can then be applied to individuals from unknown groups following the same procedure to predict group membership (Tabachnick and Fidell, 2007). Marklevitz et al. (2011) used nine trace element (Mg, K, Mn, Fe, Zn [^{67}Zn], Rb, Sr [^{88}Sr], Ba and Pb) concentrations in otoliths from 13 to 16 juvenile Chinook salmon collected in the 24 natal sources to create a LDFA model for assigning natal site. In this analysis, data for eight trace elements (Mg, K, Mn, Zn, Rb, Sr, Ba and Pb) were normalized using log transformations. Hereafter, this model will be referred to as the Marklevitz et al. (2011) model.

Three assumptions must be made when using the Marklevitz et al. (2011) model to predict natal sources of adult Chinook salmon in Lake Huron: 1) all natal sources of Chinook salmon in the fishery were included in the model; 2) there is no temporal variability in otolith microchemistry of Chinook Salmon from Lake Huron rivers and hatcheries; and 3) the juvenile section in adult otoliths can be consistently isolated and analyzed. Violations to assumptions 1 and 2 are highly likely. While efforts were made by Marklevitz et al. 2011 to sample major natal sources of Chinook salmon in Lake Huron, it is unlikely that all sources of Chinook salmon in Lake Huron were sampled. For example, Chinook salmon have previously been observed spawning on a lake trout spawning shoal, but contributions to the fishery are unknown and assumed to be minimal (Powell and Miller, 1990). Hatchery and naturalized Chinook salmon could also potentially migrate from Lake Michigan but if such migration occurs it appears to be negligible (Adlerstein et al. 2007, 2008). Temporal variability in otolith microchemistry is also likely (Pangle et al.

2010; Tanner et al. 2012). In fact, Marklevitz et al. (2011) suggested that within-year temporal variability in otolith microchemistry likely reduced site-specific assignment accuracy from the training dataset (87%) to a test dataset (23%). However, high accuracy (93%) was achieved in the test dataset by pooling assigned sites into broader spatial regions which included sites in geographical proximity (< 150 km) and/or sites with similar geology. These results demonstrate that pooling site-specific assignments into regions can result in improved assignment accuracy, robust to violations in assumptions 1 and 2. This means that the grouping of site-specific assignment into region will likely compensate for fish originating from any unknown origins within a region and any temporal variability within natal sources. In this study, site-specific assignments of adult fish were pooled into natal regions based on geographical proximity (< 150 km) and/or sites with similar geology and named based on the statistical district at the river outlets (Figure 4.2). The Northern Huron (NH_n; subscript denotes “natal”) region includes NC1-3, MH1-6, and OH1-2; the Central Huron (CH_n) region includes OH3; the Southern Huron (SH_n) region includes OH4-5; and the Georgian Bay (GB_n) region includes GB4.

The ability to predict the natal source of adult Chinook salmon was validated using the Marklevitz et al. (2011) model by examining assignments of adults captured in the Sydenham and Beaver Rivers in 2007 and 2010 ($n = 65$) and OTC-marked fish captured in the 2010 fishery ($n = 84$). Because Chinook salmon accurately home to natal locations to spawn (e.g., Quinn and Fresh, 1984), adults with adipose fin clips captured within the Sydenham or Beaver Rivers were assumed to have originated from the local Sydenham Sportsmen’s Association hatchery; fish without adipose fin clips were assumed to have originated as naturalized juveniles (age-0) from these rivers. Ninety-four percent of fish captured in the Sydenham and Beaver Rivers were correctly assigned to the Georgian Bay natal region (79% in 2007 and 100% in 2010). The misassignments in 2007 were to the Platte River Hatchery (five fish), Gore Bay Fish and Game Club hatchery (one fish), Maitland River (two fish), Sauble River (four fish), and Saugeen River (two fish). The Marklevitz et al. (2011) model did not perform well for identifying adult hatchery fish. In 2010, 21 adults from the Sydenham River and one adult from the Beaver River were hatchery fish. Whereas 81% of these fish were correctly assigned to Georgian Bay as their natal region, none were assigned to Sydenham Sportsmen’s

Table 4.2: Summary of how natal sites (rivers and hatcheries) were nested within each natal region. Numbers correspond to locations in Figure 4.1.

Natal region	Natal river	Natal hatchery
NH _n	(1) Nunns Creek, MI	(18) Thompson State, MI
	(2) Carp River, MI	(19) Platte River State, MI
	(3) St. Marys River, MI/ON	(20) Wolf Lake State, MI
	(4) Root River, ON	(21) Gore Bay Fish and Game Club, ON
	(5) Garden River, ON	
	(6) Lauzon Creek, ON	
	(7) Spanish River, ON	
	(8) Kagawong River, ON	
	(9) Mindemoya River, ON	
	(10) Manitou River, ON	
CH _n	(11) Saugeen River, ON	(22) Lake Huron Fishing Club, ON
	(12) Sauble River, ON	
SH _n	(13) Maitland River, ON	(23) Bluewater Anglers, ON
GB _n	(14) Sydenham River, ON	(24) Sydenham Sportsmen's Association, ON
	(15) Bighead River, ON	
	(16) Beaver River, ON	
	(17) Nottawasaga River, ON	

Association hatchery. Of the Michigan hatchery fish, only 12% were assigned to Michigan hatcheries. An additional 18% were assigned to an Ontario hatchery (Gore Bay Fish and Game Club hatchery) in the Northern Huron natal region. The remaining fish were assigned to various rivers within Northern Huron (9%), Central Huron (39%) and Georgian Bay (21%) natal regions. Michigan hatchery fish are reared and stocked in different watersheds, a practice different than Ontario hatcheries which rear and stock within the same river watershed. Validation therefore appears to suggest that stocking practices influence microchemistry in the juvenile section of otolith I analyzed; this will be further discussed. Given the identified limitations of the Marklevitz et al. (2011) model, OTC marks were used as a definitive indicator for assigning natal sources of Michigan hatchery fish. Michigan hatchery fish were subsequently assigned to NH_n because 75% of the fish stocked by the State of Michigan into Lake Huron between 2004 and 2010, were released along the coast in NH_c (Figure 4.1; FWS/GLFC, 2010). The other 25% of Michigan stocked fish were released at varying locations in CH_c and SH_c. However, with low survival of age-0 Chinook salmon in CH_c and SH_c contributions to the fishery were assumed to be minimal (unpublished data, J. Johnson).

L DFA was used to assess whether $^{87}\text{Sr}/^{86}\text{Sr}$ ratios could discriminate fish based on their rearing environment (hatchery versus naturalized), rearing site and bedrock geology (Carboniferous, Devonian, Silurian, Ordovician, and Precambrian; see Marklevitz et al. 2011 for a map of the geological regions). L DFA models were first developed using the subset of juveniles collected for the Marklevitz et al. (2011) study. For these models, overall assignment accuracies are presented. If the model had high classification accuracy, the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of adult fish were applied to a DFA model to assign natal locations.

4.2.4 Spatial and temporal variability in sample composition

Fish were collected from a subset of the capture regions in the same time period in both years (Northern Huron in spring, early summer, and late summer and Southern Huron in spring), and thus were used to evaluate if years could be pooled for spatial comparisons of otolith chemistry and sample composition (Figure 4.1). Within years, it was possible to compare capture regions in spring (2008 and 2010), early summer (2010),

and late summer (2010). It was also possible to compare capture periods for the Northern Huron fishery (2008 and 2010), the Central Huron fishery (2010), and the Southern Huron fishery (2010). Multivariate analysis of variance (MANOVAs) models were used for comparisons of otolith microchemistry (logMg, logK, logMn, Fe, logZn, logRb, logSr, logBa and logPb; Marklevitz et al. 2011). MANOVAs used the full variability in otolith microchemistry to test for differences in sample composition. Significant MANOVAs alone do not indicate differences in natal sources because there may be temporal variability in site-specific otolith microchemistry. Therefore, Chi-square (χ^2) tests for independence were used to compare composition of fish from the different natal regions among samples based on Marklevitz et al. (2011) model assignments and/or hatchery markings. The southern Huron natal region was excluded from χ^2 analyses of sample composition because of their rare occurrence in the samples (< 4%). This was done to reduce the number of expected values in contingency tables that fell below five (Zar, 2010).

4.2.5 Lake wide sample composition

Sample composition was estimated separately using fish captured in the 2008 ($n = 79$) and 2010 ($n = 402$) fisheries. To estimate sample composition (% contribution by each natal region) with 95% confidence intervals (C.I.s), bootstrap procedures with 1,000 iterations were performed (Manly, 1997). For 2010 only, sample composition was analyzed separately for hatchery and naturalized fish. In addition, χ^2 tests for independence were used to test if lake wide sample composition differed between years or between hatchery and naturalized fish in 2010. The Southern Huron natal region was excluded from χ^2 analyses of lake wide sample composition. Four fish sampled in 2010 lacked identification of rearing environment (hatchery or naturalized) and were excluded from this analysis. In 2008, naturalized and hatchery fish could not be distinguished with certainty due to the absence of hatchery marks on many age-3 and age-4 fish. Monte Carlo simulation was used to estimate p-values when expected values in the contingency tables fell below five (Sheskin, 2007; Zar, 2010).

4.2.6 Sensitivity analysis of regional assignments

Sensitivity analysis was performed to assess the robustness of assigned natal regions, given the uncertainty in site-specific assignments. In the current study, the Marklevitz et al. (2011) model produced $\max\{p_{\text{assign}}\}$ values in adult fish ranging from 0.25 to 1.0 ($n = 481$). Few otolith microchemical studies consider uncertainty in site assignments prior to the interpretation of results (Munch and Clarke, 2008), although a previous study used a $\max\{p_{\text{assign}}\} < 0.50$ criteria to assign fish to an “unknown origin” (Boehler et al. 2012). Alternatively, to assigning an unknown origin to these cases and effectively removing these samples from analyses, p_{assign} values were used as weighting factors in the estimation of stock composition to obtain $\text{weighted}\{p_{\text{assign}}\}$ values. The probability ($p_{i,j}$) that an individual fish (i) originated from each natal region (j ; NH_n, CH_n, SH_n, or GB_n) was calculated as:

$$p_{ij} = \sum p_{\text{assign},k(j)}$$

where k is the natal site. Note that for individual fish, $\sum p_{\text{assign},k} = 1$. For all Michigan hatchery fish, p_{assign} for $j = \text{NH}_n$ was set to 1.0, because the Marklevitz et al. (2011) model was not used to assign a natal source to these fish. The estimated number of fish originating from each natal region j was then calculated by summing the p_{ij} values.

4.3 Results

4.3.1 Spatial and temporal variability in sample composition

There was evidence to support spatial heterogeneity in sample composition of Chinook salmon from the 2008 and 2010 fishery (Table 4.3). In 2010, assigned natal region was not independent of the capture region for all fish ($\chi^2 = 220$, $df = 6$, $p < 0.0001$), hatchery fish alone ($\chi^2 = 158$, $df = 6$, $p < 0.0001$), or naturalized fish alone ($\chi^2 = 103$, $df = 6$, $p < 0.0001$; Table 4.4). Similarly, hatchery composition (hatchery versus naturalized) was not independent of capture region ($\chi^2 = 41.2$, $df = 6$, $p < 0.0001$; Table 4.4). Almost all (99%) of the fish originating from Northern Huron rivers and hatcheries were captured in Northern Huron. Fish originating from Central Huron rivers and hatchery were captured in Northern Huron (53%) and Southern Huron (28%) regions. Whereas the majority

(82%) of hatchery fish from Georgian Bay were captured in Georgian Bay, naturalized fish originating from Georgian Bay rivers were captured in all regions.

Years could not be pooled to test for spatio-temporal differences in otolith microchemistry and sample composition. Otolith microchemistry differed between years in Northern Huron during spring (MANOVA: $F_{9,19} = 85.9, p < 0.0001$), early summer ($F_{3,82} = 13.5, p < 0.0001$) and late summer ($F_{9,167} = 14.3, p < 0.0001$) and in Southern Huron during spring ($F_{9,35} = 33.0, p < 0.0001$). These between-year differences corresponded to differences in sample composition among capture regions or capture periods (Table 4.4, Figure 4.2). For example, in Northern Huron, where the overall catch was dominated by fish originating from Northern Huron hatcheries and rivers, there were more fish originating from the Georgian Bay natal region in the spring of 2008 (~80%) than in the spring of 2010 (~21%; $\chi^2 = 12.8, df = 2, p = 0.0017$; Figure 4.2). During spring in Southern Huron, there were more fish originating from the Northern Huron natal region in 2008 (58%) than in 2010 (0%; $\chi^2 = 19.4, df = 2, p < 0.0001$). Thus, in Central and Southern Huron, the overall catch was dominated by fish originating from Northern Huron in 2008 but Georgian Bay in 2010 (Figure 4.2).

Table 4.3: Summary of spatio-temporal comparisons of otolith microchemistry, sample composition and hatchery composition (hatchery: naturalized) for samples of Chinook salmon collected from the 2008 and 2010 Lake Huron fishery. MANOVAs tested for differences in microchemistry (nine trace element concentrations: logMg, logK, logMn, Fe, logZn, logRb, logSr, logBa, and logPb). Chi-Square (χ^2) tests for independence assessed differences in sample composition based on natal regions and hatchery composition (2010 only). Refer to Table 4.1 for capture regions and capture periods included in particular comparisons.

Comparison	Otolith microchemistry	Stock composition	Hatchery composition
2008			
Capture regions in spring	$F_{18,76} = 5.93^{**}$	$\chi^2_6 = 21.8^*$	N/A
Capture periods in Northern	$F_{18,68} = 8.08^{**}$	$\chi^2_6 = 23.6^*$	N/A
Huron			
2010			
Capture regions in spring	$F_{9,30} = 4.22^*$	$\chi^2_3 = 24.8^*$	$\chi^2_2 = 0.21$
Capture regions in early summer	$F_{9,99} = 26.3^{**}$	$\chi^2_2 = 37.8^*$	$\chi^2_2 = 3.38$
Capture regions in late summer	$F_{9,704.49} = 15.4$ **	$\chi^2_6 = 145^*$	$\chi^2_6 = 9.43$
Capture periods in Northern	$F_{18,484} = 5.67^{**}$	$\chi^2_4 = 2.88$	$\chi^2_1 = 15.4^*$
Huron			
Capture periods in Central Huron	$F_{9,26} = 2.18$	$\chi^2_1 = 0.93$	$\chi^2_1 = 0.012$
Capture periods in Southern	$F_{9,22} = 3.89^*$	$\chi^2_2 = 0.80$	$\chi^2_1 = 0.002$
Huron			

* $0.05 > p > 0.0001$, ** $p < 0.0001$

Table 4.4: Sample composition (%) by capture region of naturalized and hatchery Chinook salmon in the 2010 Lake Huron recreational fishery. Rows represent proportions of adult fish from each natal region and rearing environment (naturalized or hatchery) based on Marklevitz et al. (2011) model assignments and/or hatchery markings. Columns represent capture region. Total number of fish assigned to each natal region are presented.

Natal region	Capture region				Total
	Northern Huron	Central Huron	Southern Huron	Georgian Bay	
Naturalized					
Northern Main Basin	0.99	0	0	0.01	92
Central Main Basin	0.54	0.08	0.23	0.15	26
Southern Main Basin	0	0	1.00	0	1
Georgian Bay	0.34	0.21	0.13	0.31	145
Hatchery					
Northern Main Basin	1	0	0	0	90
Central Main Basin	0.50	0	0.50	0	6
Southern Main Basin	0	0	0	0	0
Georgian Bay	0.05	0.08	0.05	0.82	38

* The Southern Main Basin natal region is displayed for reference but was not included in the χ^2 tests for heterogeneity.

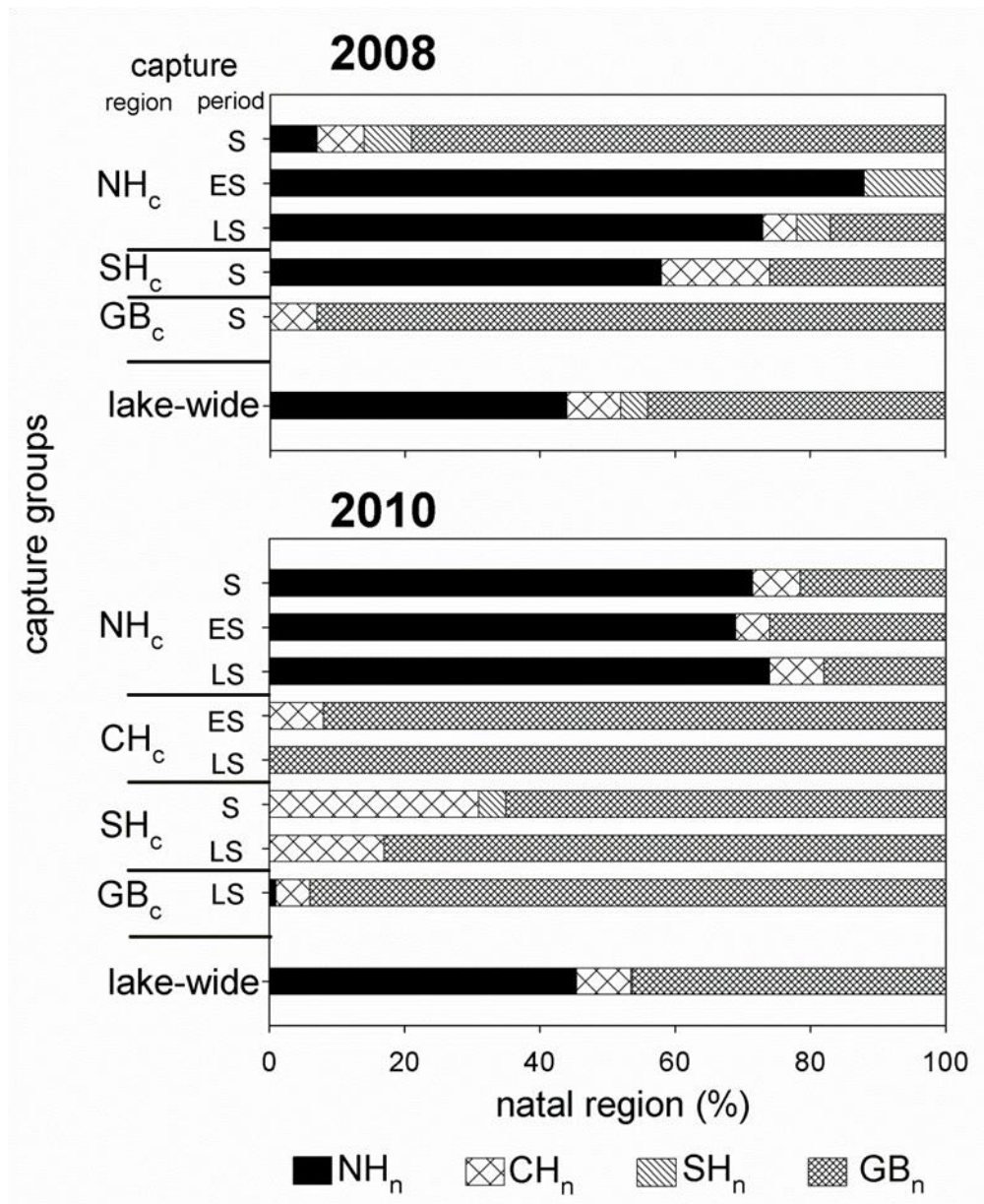


Figure 4.2: Spatio-temporal capture patterns of Chinook salmon by natal region (NH_n, CH_n, SH_n, and GB_n) in the 2008 and 2010 Lake Huron recreational fishery. Horizontal bar represents proportion of fish from each natal region based on Marklevitz et al. (2011) model assignments and/or hatchery markings, captured in each spatio-temporal capture groups. For samples sizes, see Table 4.1.

Lake wide sample composition

Lake wide, sample composition showed broad similarity between years (Table 4.5). Combining 2008 and 2010, the contributions by natal region were as follows: $NH_n = 183$ (46%), $CH_n = 33$ (8%), $SH_n = 1$ (0.2%), $GB_n = 185$ fish (46%). In 2010, naturalized fish ($n = 264$) comprised 66% of fish sampled lake wide ($n = 398$). Naturalized fish originated predominately from Georgian Bay (55%) and Northern Huron (35%) rivers in 2010 (Table 4.5). Central and Southern Huron rivers contributed fewer fish (9% and <1%, respectively). The majority (67%) of hatchery fish ($n = 134$) originated in 2010 from Northern Huron hatcheries (US hatcheries and Gore Bay Fish and Game Club hatchery) (Table 4.5). Georgian Bay and Central Huron hatcheries contributed fewer (28% and 4%, respectively) of the hatchery fish sampled.

Otolith $^{87}\text{Sr}/^{86}\text{Sr}$ was useful for discriminating natal locations from the Precambrian geological region. Mean $^{87}\text{Sr}/^{86}\text{Sr}$ ratios were $0.7091 \pm \text{SD} = 0.0009$ ($n = 25$) for the Carboniferous, 0.7095 ± 0.0004 ($n = 10$) for the Devonian, 0.7091 ± 0.0011 ($n = 84$) for the Silurian, 0.7099 ± 0.0008 ($n = 24$) for the Ordovician and 0.7179 ± 0.0035 ($n = 28$) for the Precambrian regions. Otolith $^{87}\text{Sr}/^{86}\text{Sr}$ was higher in the Precambrian region and increasing $^{87}\text{Sr}/^{86}\text{Sr}$ was evident from west to east: e.g., Root River (0.7136 ± 0.0002 ; $n = 6$) to Lauzon Creek (0.7170 ± 0.0004 ; $n = 14$) to the Spanish River (0.7228 ± 0.0011 ; $n = 8$). Non-Precambrian sites (dominated by marine carbonate sedimentary rocks) are statistically indistinguishable from each other and similar to modern seawater ($^{87}\text{Sr}/^{86}\text{Sr}$ of 0.70917). The LDFA model to discriminate juveniles from the east Precambrian (Lauzon Creek and Spanish River), west Precambrian (Root River) and younger (Carboniferous, Devonian, Silurian, and Ordovician) bedrock resulted in a very high classification accuracy, 97% (i.e., 168/171 were correctly classified). The other LDFA models had much lower classification accuracy. The site-specific LDFA for juveniles resulted in an assignment accuracy of 53%, and the hatchery vs. naturalized LDFA resulted in an assignment accuracy of 70%. For the 102 adult samples that were tested with the 3-level, bedrock-specific LDFA model, one was assigned to the east Precambrian region (i.e., Lauzon Creek and Spanish River), six were assigned to the Root River, and 95 were assigned to regions with younger bedrock. Assuming these adult samples are

Table 4.5: Estimated contribution (%) by natal region of Chinook salmon in the 2008 and 2010 Lake Huron recreational fishery. Means with 95% confidence intervals (in brackets) were calculated by bootstrap resampling (1000 iterations) fish opportunistically but representatively sampled from the recreational fishery. Non-overlapping 95% confidence intervals indicate significant differences. Estimated sample contribution (%) of naturalized and hatchery fish by natal region are calculated for 2010.

Sample	Natal region			
	Northern Huron	Central Huron	Southern Huron	Georgian Bay
2008	0.45 (0.34- 0.56)	0.08 (0.03 – 0.14)	0.04 (0.01 – 0.09)	0.44 (0.34 – 0.54)
2010	0.45 (0.41 – 0.50)	0.08 (0.6 – 0.11)	0.004 (0.002 – 0.008)	0.46 (0.41 – 0.51)
Naturalized	0.35 (0.29 – 0.41)	0.09 (0.06 – 0.14)	0.006 (0.004 – 0.015)	0.55 (0.49 – 0.61)
Hatchery	0.67 (0.60 – 0.75)	0.04 (0.01 – 0.09)	-	0.28 (0.21 – 0.36)

representative of the entire sample, < 1% of the naturalized fish from the lake wide sample were estimated to originate from rivers on the Canadian Shield east of the St. Marys River. Therefore, for the naturalized fish originating from the Northern Huron region, the vast majority likely originated from tributaries flowing from Ontario into the St. Marys River (e.g., Garden River and Root River), Upper Peninsula of Michigan (e.g., Carp River and Nunn's Creek, both adjacent to MH-1) and Manitoulin Island (e.g., Kagawong, Manitou and Mindemoya Rivers, all adjacent to OH-1 and NH-2).

4.3.2 Sensitivity analysis of regional assignments

Sensitivity analysis demonstrated that the assigned natal regions of fish based on $\max\{p_{\text{assign}}\}$ from the Marklevitz et al. (2011) model, in combination with hatchery marks, produced robust results despite uncertainty in site-specific natal source assignments. In 2008, the estimated numbers of fish from each natal region based on $\max\{p_{\text{assign}}\}$ and $\text{weighted}\{p_{\text{assign}}\}$ were the same. In 2010, the estimated numbers of fish from natal regions differed by one fish.

4.4 Discussion

This study revealed spatio-temporal incomplete mixing of Chinook salmon from natal regions throughout Lake Huron and significant inter-basin migration. Two notable findings were the frequency of Michigan-hatchery fish caught in Michigan waters of Lake Huron (NH_c) and the frequent captures of Georgian Bay origin fish in the Main Basin. These results provide the first evidence directly contradicting previous assumptions of a well (completely) mixed Chinook salmon fishery (Adlerstein et al. 2007; Johnson et al. 2010). Furthermore, these findings demonstrate violations of two of five assumptions (i.e., completely mixed fishery and no immigration into the Main Basin) of a Statistical Catch-At-Age (SCAA) model used to estimate Chinook salmon abundances in Lake Huron (Brenden et al. 2012). Given the heavy dependence of the SCAA on data collected from the Michigan waters of Lake Huron (i.e., Michigan creel surveys at index ports and the Swan River weir), our findings suggest that the model likely underestimates contributions of naturalized fish in the fishery. This means that contributions from naturalized populations could have exceeded the 790,000 recruits per year in the early

1990s and 10 million recruits per year in the early 2000s predicted by the SCAA model. Therefore, the observed declines of the early 2000s in the Chinook salmon fishery in Lake Huron may have been much greater than previously thought.

Incomplete mixing of Chinook salmon from different natal regions was likely caused, in part, by population-specific movement behavior. For example, Chinook salmon originating from Georgian Bay were frequently captured in the Main Basin, whereas fish originating from outside of Georgian Bay were rarely captured in Georgian Bay. Aggregation of fish into the Northern Main Basin is consistent with it being a habitat with high abundance of preferred prey (Adlerstein et al. 2007). In the Great Lakes, Chinook salmon primarily prey on alewife, but also consume bloater (*Coregonus hoyi*), rainbow smelt (*Osmerus mordax*), round gobies (*Neogobius melanostomus*) and *Diporeia* spp. (Diana, 1990; Dobiesz et al. 2005; Jacobs et al. 2013). In Lake Huron, large proportions of the lake wide biomass of the Chinook salmon prey species are found in the northern regions of the lake (Warner et al. 2009; Barbiero et al. 2011). Moreover, one must consider proximity to northern Lake Michigan's abundant alewife and inter-lake movements of Chinook salmon via the Straits of Mackinac (Adlerstein et al. 2007). The spatial extent of in-lake movements may also be lower than assumed, leading to the capture of Chinook salmon in proximity to their natal sources. In the ancestral population from Puget Sound (Green River, Washington, US), Chinook salmon generally have short migratory ranges (0 - 700 km) compared to other nearby coastal populations (1200 - 1700 km) (Weeder et al. 2005; Weitkamp, 2010). There is also evidence that some Puget Sound Chinook salmon remain resident in Puget Sound (Quinn et al. 2011).

Capture patterns differed between hatchery and naturalized Chinook salmon originating from Southern Georgian Bay. Whereas hatchery fish from the Sydenham Sportsmen's Association in Georgian Bay were mostly captured in Georgian Bay, naturalized fish were captured in Main Basin fisheries. The opportunistic, non-random sampling of the recreational fishery conducted in this study cannot be excluded as an explanation for these results. All of the sampling in southern Georgian Bay was done in proximity to the Sydenham River, and hatchery fish make up a large proportion of the spawning population. In contrast, most of the naturalized fish from this region are thought to originate from tributaries of the Nottawasaga River (Johnson et al. 2010) and perhaps

the Bighead River (unpublished data, OMNRF). If fisheries were sampled closer to the outlet of the Nottawasaga River, then the proportion of naturalized fish would have likely been higher. Other studies do not observe differences in oceanic distributions of hatchery versus naturalized fish. For example, Weitkamp (2010) found no differences in the capture patterns of wild and hatchery Chinook salmon along the west coast of North America; however, stocking location of fish from the same hatchery has been shown to affect oceanic distributions (Chamberlin et al. 2011; Quinn et al. 2011).

Samples were not collected using a full random-stratified sampling design. A random-stratified index netting program could have been used to spatially and temporally sample Lake Huron, enabling definitive estimations of abundances, stock composition and contributions from different natal sources. However, with the large spatial extent of Lake Huron, such a sampling program would be logistically and financially unfeasible under current management priorities. Furthermore, current index netting programs target lake whitefish and lake trout, and nets are set too deep to capture Chinook salmon. However, efforts were made to spatially and temporally stratify sample collections, including sampling from Michigan index ports (creels surveys), fishing tournaments (derbies), by-catch in the commercial fishery and volunteer collection kits disseminated to anglers. There has been a near absence of Chinook salmon fisheries in Central and Southern Main Basin since 2002 and no samples were acquired from creel surveys in these regions during the study (unpublished data, J. Johnson). Beyond the opportunistically obtained samples from fishing tournaments and creel surveys, targeted collections through commercial fisheries and volunteer kits resulted in very limited samples ($n = 20$ fish). Sample collections though space and time appears to be consistent with latitudinal increases in Chinook salmon catch rates from April to October that Adlerstein et al. (2007) associated with movements of fish from southern to northern regions of the lake. Sample collection also consistent with the spatio-temporal distribution of the fishery as assessed by anecdotal evidence of angler behaviour: spring/late summer Chinook salmon fishery in Southern Georgian Bay (unpublished data, OMNRF); and spring Chinook salmon fishery in Southern Main Basin which shifts in summer to target walleye (*Sander vitreus*) in response to declining salmon catch rates (Jake VanRooyen, Bluewater Anglers hatchery manager, pers comm.). The study findings are likely

representative of the lake wide recreational fishery given efforts to spatially and temporally stratify collections of Chinook salmon and bootstrapped (random resampling) estimates of lake wide contributions from natal regions with 95% C.I.s. However, given the limitations of opportunistic sampling, the estimates should be examined as relative contributions, forming primary estimates of regional contributions or stock composition.

Results suggest that in the 2010 recreational fishery, 55% of naturalized Chinook salmon originated from rivers in Georgian Bay with an additional 35% originating from Northern Main Basin and the North Channel rivers. These results are further supported by the independent analysis of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios. Most naturalized fish had $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that were similar to the modern marine $^{87}\text{Sr}/^{86}\text{Sr}$ ratio (0.70917), possibly because they originated from areas such as southern and western Georgian Bay, which are dominated by marine carbonate rocks. $^{87}\text{Sr}/^{86}\text{Sr}$ ratios also suggest that naturalized production is much greater in the rivers of the Upper Peninsula of Michigan, St. Marys River tributaries flowing from Ontario, and Manitoulin Island than in the rivers flowing southward from the Canadian Shield into the North Channel. While the absolute contributions from Georgian Bay, Northern Main Basin and the North Channel is likely influenced by the non-random sampling, the presence of Georgian Bay origin fish lake wide and the prevalence of Northern Huron fish caught in Northern Huron further support these regions as major natal sources of fish in the fishery. Georgian Bay and Northern Huron regions contain 82% of the known naturalized populations in Lake Huron (Johnson et al. 2010; Marklevitz et al. 2011). Likely, the majority of naturalized Chinook salmon originate from rivers in these regions because of the availability of large, groundwater rich river systems (Bence et al. 2008; Claramunt et al. 2013; Johnson et al. 2010; Johnson and Gonder, 2013). Moreover, Ontario rivers flowing into Georgian Bay and the North Channel have few barriers (e.g., dams) that prevent Chinook salmon from reaching high-quality spawning habitat (Johnson et al. 2010; Johnson and Gonder 2013). In comparison, many Michigan rivers have barriers constructed near river mouths, which limit access by spawning Chinook salmon to 53 km of the 1,836 km of cold-water riverine habitat (Gebhardt et al. 2005). A GIS based spatial model (adapted from Zorn et al. 2012) which uses landscape attributes (e.g., river barriers, elevation and stream order) also predicts high numbers of naturalized age-0 Chinook salmon emigrating from Georgian Bay and

North Channel rivers (Ed Rutherford, NOAA, pers comm.). However, the lack of gravel substrate of suitable size, low late summer discharge and frozen substrates in winter may limit spawning and early life history success in Georgian Bay and North Channel rivers flowing over the Canadian Shield.

In the 2010 recreational fishery, results suggest that 67% of hatchery Chinook salmon originate from the three Michigan hatcheries (Thompson, Platte River, and Wolf Lake State hatcheries). The four Community Fisheries Involvement Program (CFIP) hatcheries in Ontario contributed fewer fish, with 28% from the Sydenham Sportsmen's Association, 4% from the Gore Bay Fish and Game Club, 4% from the Lake Huron Fishing Club and 0% from the Bluewater Anglers. These results generally match stocking rates by region. From 2006 to 2010, more than 85% (1.4 - 1.5 million fish · yr⁻¹) of fish stocked into the lake were reared at the three US hatcheries (FWS/GLFC, 2010). During the same period, CFIP hatcheries each stocked significantly fewer fish (3% to 5% of the total stocked). There were two noteworthy discrepancies between stocking rates and sample composition. The first is the high contribution of fish from the Sydenham Sportsmen's Association hatchery, which is likely the result of non-random sampling from the recreational fishery. Most Sydenham Sportsmen's Association hatchery fish were caught late in the summer (August-October) in Owen Sound proper, close to the Sydenham River in which they were released as age-0 fish. These fish were presumably homing to their release site. The second discrepancy is a lack of fish from the Bluewater Anglers hatchery despite stocking rates similar to the other CFIP hatcheries. In addition to non-random sampling, there may be lower survival among hatchery fish stocked in the Southern Main Basin. For example, there is regional variation in the consumption of age-0 Chinook salmon by walleye and lake trout, mediated by the abundance of prey such as alewife (Johnson et al. 2007; Brenden et al. 2012). In response to low survival of age-0 Chinook salmon in the Southern Main Basin, stocking of Chinook salmon in Michigan waters south of Rogers City, MI (located in NH_c), ceased in 2012.

In addition to non-random sampling of the recreational fishery, another limitation of this study was the inability to identify natal source to the specific hatchery or river. The DFA model was optimized for assignment accuracy based on the trace element concentrations of juvenile salmon used to develop the model. As suggested by Mercier et

al. (2011), the analytical method and the combination of elemental concentrations used to assign natal location were tested. Results show that the Marklevitz et al. (2011) model had the high assignment accuracy and similar assignment success to the random forest analysis based on Mercier et al. (2011) program. While the model lacked precision of site-specific assignment, there was good accuracy to a region based on the examination of the site-specific assignments of individual naturalized fish. This lack of precision may have been caused by temporal variability in trace element concentrations in the water and subsequently in the otolith (Pangle et al. 2010; Tanner et al. 2012). Pangle et al. (2010) suggested the development of site-specific libraries by collecting otoliths over a time period relevant for a given study. This would enable the inclusion of temporal variability in otolith microchemistry in assignment models. However, results suggest that this may not be required if broader scale assignments (e.g. regions) are sufficient for the objectives of a study. Pooling site-specific assignments of naturalized fish into regions was highly accurate and robust to the uncertainty in site-specific assignments.

One important limitation which could not be overcome was an inability to identify hatchery fish based on otolith microchemistry alone. Neither multi-trace element concentrations nor $^{87}\text{Sr}/^{86}\text{Sr}$ could differentiate hatchery from naturalized fish with accuracy. This inability may have been caused by the mixing of the imprinted microchemical signals from natal hatchery and release site in the juvenile otolith section. The mixing of the imprinted microchemical signals would be consistent with the observation of regional accuracy in Georgian Bay hatchery fish and the lack of regional accuracy in Michigan hatchery fish. Georgian Bay hatchery fish are reared and released in the same river watershed while all Michigan hatchery fish are reared and released in different river watersheds. In the absence of a good candidate natural marker, a priori identification of hatchery fish is needed. This may be accomplished from the continued physical marking of hatchery fish via fin clipping, oxytetracycline marking or otolith microstructure analysis (Smith et al. 2006). Despite the limitation of site-specific assignment precision, the regional assignment accuracy of naturalized fish provides valuable information at a spatial scale useful for fisheries management.

The introduced Chinook salmon in Lake Huron and the other Great Lakes have been under-studied, leading to a lack of knowledge about their basic ecology. Otolith

microchemistry is a useful tool, which enables evaluation of the assumption of a mixed-stock fishery by assessing the regional contributions of fish to the fishery. This study demonstrates that Chinook salmon from various natal sources mix incompletely in Lake Huron, contrary to previous assumptions of a completely mixed fishery (Adlerstein et al. 2007; Johnson et al. 2010; Brenden et al. 2012). There is also evidence of significant inter-basin movement from Georgian Bay into the Main Basin of Lake Huron. This study is also the first to estimate relative contributions of different naturalized populations to the lake wide fishery. Results suggest that the majority of naturalized fish in the lake wide fishery originated from rivers in Georgian Bay, Northern Main Basin and North Channel. Supplementary analysis of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios further supported this result and suggests that few naturalized fish came from the northern region rivers east of the St. Marys River.

This study addressed several priority questions and knowledge gaps of spatial ecology of Great Lakes fishes including movements within and between basins and spatial contributions/movements of stocked fish (Landsman et al. 2011). Future research and monitoring of Chinook salmon in the Great Lakes is needed to evaluate population-specific differences in movement patterns and lake wide seasonal distributions. A better understanding of the spatial ecology of Chinook salmon is needed so that it may be incorporated into fisheries models (e.g., Brenden et al. 2012: SCAA model). For example, findings of this study do not support two assumptions used in the model to estimate Chinook salmon abundances in Lake Huron (Brenden et al. 2012). These potential violations could lead to underestimates of naturalized fish abundances and subsequently age-0 natural mortality rates of these fish. Therefore, better understanding the spatial ecology of Chinook salmon in Lake Huron and the other Great Lakes is critical for the sustainable management of the fisheries and lake ecosystems.

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5 General Discussion

The intentional introduction, establishment of naturalized populations and continued stocking of non-native Chinook salmon into the Great Lakes provides a unique and interesting opportunity for fisheries research. It provides a natural experiment from which studies of local adaptation and evolution in salmonids, successful stocking programs leading to established naturalized populations, the effects of prolonged and intensive stocking programs and broad scale ecosystem manipulation (i.e., food web management) can be conducted. It also presents an interesting paradigm for fisheries management in how to sustainably manage a purposely introduced and stocked non-native species. The United Nations defines sustainability or sustainable development as a balance between the environment, society and economy to meet the needs of today (the present) while not compromising the needs of the future (United Nations, 1987). Fisheries are inherently biological, social and economic structures, so unsustainable practices that compromise the environment also threatens food security, cultural identity and economic welfare of the regions and people that rely on fisheries (Smith et al. 2010). Thus to sustainably manage fisheries, a careful balance must be maintained between the long term ecological integrity and the social and economic wants and needs (Hilborn and Walters, 1992).

The importance of Chinook salmon fisheries in the Great Lakes are reflected in the Great Lakes Fishery Commission (GLFC) fish community objectives (FCOs) for Lakes Superior (Horns et al. 2003), Michigan (Eshenroder et al. 1995), Huron (DesJardine et al. 1995) and Ontario (Stewart et al. 2013). In fact, Lake Michigan FCOs specifically set a 3.1 million kg · year⁻¹ target for Chinook salmon catches (Eshenroder et al. 1995). Lake Ontario FCOs specifically states “maintaining Chinook salmon as the top offshore pelagic predator” is a priority (Stewart et al. 2013). The Lake Huron FCOs are less explicit, setting targets of 2.4 million kg · year⁻¹ for all salmonid catches “with lake trout the dominant species and anadromous (river spawning) species (including Chinook salmon) also having a prominent place” (DesJardine et al. 1995). With the significant contributions of naturalized Chinook salmon to Great Lakes fisheries, continued achievement of these FCOs is going to require a fundamental shift from maintaining abundances solely through stocking rates to understanding the dynamics of naturalized

populations. In addition, we need to consider if these FCOs are sustainable, with the fisheries now supported predominately by naturalized populations.

The presence of Chinook salmon in the Great Lakes has had complex environmental, social and economic effects with conflicting views on the costs and benefits (Kocik and Jones, 1999; Crawford, 2001; Claramunt et al. 2013). On one hand (enhancement view), Chinook salmon occupy a mid-water pelagic piscivore niche created by abundant invasive foraging species, alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) and near absence of native piscivores, lake trout (*Salvelinus namaycush*). Their successful re-establishment and maintenance of top-down control of the food web has reduced abundances of these invasive forage species across the Great Lakes Basin (O’Gorman et al. 2004; Madenjian et al. 2005, 2008; Riley et al. 2008). Subsequent recoveries of native species at all trophic levels have been linked to reductions in the invasive forage species abundances; for example, foraging species, emerald shiners (*Notropis atherinoides*); intermediate piscivore, yellow perch (*Perca flavescens*); and apex piscivore, lake trout (*Salvelinus namaycush*) (Riley et al. 2007; Schaeffer et al. 2008). Chinook salmon may further aid lake trout restoration efforts because they preferentially prey on alewife independently of the relative abundances of prey species (Diana, 1990; Jacobs et al. 2013). The composition of lake trout diets generally reflects relative prey abundances and diets high in alewife can elevate thiamine deficiencies in eggs and early mortality syndrome in offspring (Miller and Holey, 1992; Honeyfield et al. 2005; Fitzsimons et al. 2007). The presence of Chinook salmon has also created new multimillion-dollar recreational fisheries for large, charismatic species that are highly desired by recreational fishers. These new fisheries have had significant social and economic benefits for otherwise depressed coastal communities (Claramunt et al. 2013; Thayer and Loftus, 2013).

On the other hand (restoration view), non-native Chinook salmon represent the introduction of an abundant potamodromous (migrate from lakes to rivers to spawn), semelparous (breed once then die) fish species into ecosystems where such life histories were minimal (Crawford, 2001). This raises concerns of interspecific competition with native species and ecological effects within the Great Lakes and their tributaries. For example, spawning Chinook salmon in the native range can affect sediment particle size,

dissolved nutrients, benthic macroinvertebrates, biofilms and the riparian ecosystems in rivers through environmental engineering effects during nest construction and decomposition of carcasses (Naiman et al. 2002; Janetski et al. 2009). Direct interactions between Chinook salmon and native species in the Great Lakes Basin is poorly understood (Crawford, 2001). Within the lakes, there is concern the Chinook salmon may compete with native lake trout and potentially impede restoration efforts (Crawford, 2001; Roseman and Riley, 2009).

Regardless of individual opinion, understanding stock structure of the fisheries and habitat use in rivers and lakes is critical to understanding Chinook salmon ecology in the Great Lakes and sustainably managing this introduced species. Ecologically, there are implications on foraging, competition (intra- and inter-specific), reproduction, and exposure to predation, parasitism, disease, anthropogenic activities and fisheries of varying intensities (Quinn, 2005). For sustainable management of the fisheries, in addition to the ecological considerations, stock structure and habitat use forms the basis of defining management units, design and implementation of assessment programs, interpretation of changes in the fishery and results of assessment models, and the coordination or allocation of multi-agency management strategies, policies and enforcement (Hilborn and Walters, 1992). The assumption that indefinite stocking would be required to sustain the fisheries has resulted in a lack of research or monitoring of naturalized populations or consideration of the effects of continued stocking (Crawford 2001; Claramunt et al. 2013). In the absence of basic ecological information, researchers and managers have been forced to make broad and potentially oversimplified assumptions, including similarities in the survival and habitat use of hatchery and naturalized fish and completely mixed in-lake fisheries. These over simplified assumptions may have led to overstocking in the presence of significant amounts of naturalized reproduction (Roseman and Riley 2009; Johnson et al. 2010; He et al. 2015).

My Ph.D. research provides the first individual level examination of river (spawning) and lake (foraging) habitat use by naturalized and hatchery Chinook salmon in the Great Lakes. I identified origins of naturalized fish, identified how naturalized and hatchery fish contribute to a spawning population and the Lake Huron fishery, and compared habitat use during spawning and foraging between difference sources. With this

new information, my research has begun to address knowledge gaps required to properly understand and model population dynamics and sustainably manage the fishery.

5.1 Spawning habitat use

Prior to my research, there was almost no research or monitoring of Chinook salmon in Great Lakes tributaries except some surveys for naturalized populations (e.g., Carl, 1982; Kerr and Perron, 1986, Marklevitz et al. 2011) and factors affecting the survival of hatchery fish released into rivers (Johnson et al. 2007). My Ph.D. research demonstrated that hatchery fish were a significant (> 50%) component of the fish returning to spawn in the Sydenham River (Chapter 2). Chinook salmon regardless of origin (hatchery or naturalized) or sex moved and spawned extensively throughout the accessible river despite evidence of accurate and precise homing to the stocking site by hatchery females.

The significant number (> 50%) of hatchery fish returning to the Sydenham River provides evidence of accurate natal homing by hatchery fish to natal rivers. This finding is consistent with early studies testing the olfactory imprinting hypothesis for natal homing on another introduced Pacific salmonid species (coho salmon, *Oncorhynchus kisutch*) in Lake Michigan (Horrall, 1981). Nack et al. (2011) also found significant contributions of hatchery fish (68%) in the annually stocked Salmon River (New York) flowing into Lake Ontario. We know very little about homing and straying rates of Chinook salmon to rivers in the Great Lakes except straying must be occurring at levels that facilitated the colonization and formation of naturalized populations (Suk et al. 2011). Research on sockeye populations on the West Coast of North America have demonstrated that straying fish are often found in or at natal river mouths prior to spawning in non-natal rivers, while homing fish are not often observed in non-natal rivers prior to spawning (Peterson et al. 2015). Research suggested fish stray in response to environmental conditions and abundances of fish returning to natal rivers (Clobert et al. 2009; Peterson et al. 2015). Homing and straying rates among populations in the Great Lakes and the influence of stocking is an important future research direction as it highly influences genetic structure of populations (e.g. Weeder et al. 2005; Suk et al. 2011) and

evolutionary adaptation of Chinook salmon to novel environmental and climatic conditions.

The significant numbers of individuals returning to spawn in the Sydenham River should concern fisheries managers because it may exceed the natural environmental carrying capacity. Previous research and monitoring in the Great Lakes has primarily been concerned about the potential of stocking to increase interspecific competition with lake trout and effects on the predator-prey balance in the lakes (e.g., Roseman and Riley, 2009; He et al. 2015). Stocking could also increase abundances in spawning habitat with the potential to suppress productivity of naturalized populations. When environmental carrying capacities in spawning rivers are exceeded, density-dependent feedback mechanisms intensify reducing reproductive success of individuals (Milner et al. 2003). A previous survey of the Sydenham River had estimated enough habitat to support approximately 200 pairs of spawning salmon (John Bittorf, Grey Sauble Conservation Authority, pers comm.). This was approximately the numbers of naturalized females observed returning in 2010 ($n = 214$) and 2011 ($n = 197$) (Chapter 2). Hatchery fish (2010 = 270; 2011 = 339) more than double the number of potential spawning pairs each year. In the Sydenham River, Gerson et al. (2016) indeed observed evidence of active density-dependent mechanisms in females including egg retention and nest superimposition (Kinnison et al. 1998; Quinn et al. 2007; Schroder et al. 2008). This may result in unpredicted responses to reductions in stocking, such as increasing reproductive success of naturalized spawning individuals. Further research is needed to understand the sizes of populations and carrying capacity of the many other Great Lakes tributaries such as Salmon River, Credit River and Bronte Creek in Lake Ontario, Saugeen, Beaver, Bighead and Nottawasaga Rivers in Lake Huron, and the Pere Marquette, Manistee and Muskegon Rivers in Lake Michigan, and how density-dependent effects caused by stocking programs may affect the productivity of these populations.

Similarities in spawning habitat use by hatchery and naturalized fish mean that hatchery and naturalized Chinook salmon in the Sydenham River lack reproductive isolation by time or distance (Hendry and Day, 2005; Dittman et al. 1996). Hatchery fish have been shown to have altered behaviours and phenotypic traits (i.e., smaller sizes, lower fecundity) that are detrimental to their reproductive success and that of the

naturalized fish with which they spawn (Fleming et al. 1996; 1997; Knudsen et al. 2006, 2008; Schroder et al. 2008, 2010, 2012). Interbreeding between hatchery and naturalized fish can also perpetuate maladapted heritable traits across generations to the wild born offspring of hatchery parents (Araki et al. 2007, 2008, 2009). Prolonged stocking of high numbers of hatchery fish has been shown to reduce the productivity of wild populations partially attributed to perpetuation of maladapted traits (Kostow and Zhou, 2006; McGinnity et al. 2009; Chilcote et al. 2011). In the Sydenham River, one such maladapted trait may be arrival and spawning timing. Gerson et al. (2016) found evidence of a weak phenological match between Sydenham River temperature regimes and spawning timing. This weak phenological match may be caused by selection on arrival timing during gamete collections. Similar to the density-dependent issues, the lack of reproduction-isolation by hatchery and naturalized fish may result in unpredictable responses of recruitment of naturalized fish to alterations in stocking rates.

A logical step forward from my research would be a detailed examination of hatchery and naturalized interactions during spawning and the effects of these interactions on individual level reproductive success and population specific recruitment. The Great Lakes offer a unique situation in which to study the effects of prolonged stocking because all fish originate from the same ancestral population, limiting the effects caused by genetic differences among naturalized populations and hatcheries (Weeder et al. 2005; Suk et al. 2011). With the establishment of naturalized populations and continued stocking in some rivers, there are likely gradients in the influence of stocking programs among and within populations. For example, my research and others have found different contributions of hatchery fish in spawning rivers: Swan River (Michigan) > 90% (Johnson et al. 2010); Salmon River (NY) = 68% (Nack et al. 2011); and Sydenham River > 50%. Nack et al. (2011) also found differences in spatial habitat use of hatchery and naturalized fish within a spawning river, which is an indication of within population differences in hatchery influences. Examining the effects of stocking practices in the Great Lakes could provide valuable insight to help design stocking strategies for rehabilitating threatened and endangered salmon populations in their native ranges. For example, research in the Great Lakes could provide information about stocking rates, timing and location to promote natal homing and arrival synchrony that would

enhancement targeted populations (or rivers) while minimizing potential effects on other populations.

Few studies have examined the effects of Chinook salmon to river ecosystems and river-resident fish species in the Great Lakes. In the Sydenham River, the extensive movement and spawning through the assessable habitat and similarities in habitat use between rearing origins demonstrate impacts of naturalized and hatchery Chinook salmon could be substantial in accessible rivers. In the Great Lakes, increases in dissolved nutrients (soluble reactive phosphorous, dissolved organic carbon, ammonium and nitrate) and decreases in periphyton were associated with salmon spawning (Collin et al. 2011). Nutrient subsidy effects from the decomposition of carcasses appear to be weak in comparison to rivers in the native range of Chinook salmon, but sediment routing commonly reduces benthic biofilms and macroinvertebrates by 90% in Great Lakes tributaries (Collin et al. 2011; Janetski et al. 2014). Our knowledge about the effects of Chinook salmon on native species in Great Lakes tributaries remains limited. Chinook salmon appear to act as lake-to-river vectors of contaminants with river-resident fish in salmon spawning rivers displaying elevated organic pollutants such as polychlorinated biphenyls (PCBs), dichlorodiphenyldichloroethylene (DDE), and polybrominated diphenyl ethers (PBDEs) (Janetski et al. 2012). Spawning Chinook salmon may also displace some resident species, for example brook trout (*Salvelinus fontinalis*) (Janetski et al. 2011). An interesting finding was the potential for Chinook salmon to be food sources for river-resident fish through consumption of eggs or carcasses (Janetski et al. 2011; Johnson et al. 2016). These potential effects within rivers are important considerations for habitat restoration or alteration projects that influence the lake-river connectivity such as dam removals and fishway construction. Connecting habitat previously inaccessible to Chinook salmon could have significant ecological effects especially on previously isolated fish populations.

While my research and other recent studies (e.g., Nack et al. 2011; Collin et al. 2011; Janetski et al. 2012, 2014; Houde et al. 2015; Johnson et al. 2016; Gerson et al. 2016) have started to examine the ecology of Chinook salmon in Great Lakes tributaries, much remains unknown. For example, what are the straying rates among populations and hatcheries? How have Chinook salmon adapted to the novel environments of Great Lakes

tributaries? What are the effects of the prolonged and intensive stocking programs on naturalized populations? The riverine ecology of Chinook salmon remains in need of further research. Furthermore, with the reduction in stocking rates and increasing reliance of naturalized populations to sustain the fisheries, a better understanding of the river ecology of Chinook salmon is important for predicting and understanding the population dynamics of these fish in the lakes.

5.2 Foraging habitat use

In the Great Lakes region, most of our understanding of Chinook salmon including recruitment of naturalized fish comes from fisheries. Prior to my research, estimates of naturalized recruitment were derived from simple catch ratios of hatchery to naturalized fish. Fisheries models then used these ratios and metrics such as survival, natural mortality, catchability and recruitment based predominately on hatchery fish to estimate naturalized fish abundances and recruitment (e.g., Connerton et al. 2009; Johnson et al. 2010; Brenden et al. 2012; Tsehaye et al. 2014). Our only knowledge about habitat use and movement through the lake basins were also derived from coded wired tagged hatchery fish in Lakes Huron and Michigan (Adlerstein et al. 2007, 2008). There has been a lack of basic assessments of naturalized populations that did not rely on comparisons (e.g., hatchery to naturalized ratios) or directly to metrics (e.g., survival) of hatchery fish. This lack of information has resulted in undervaluation of the significance of naturalized reproduction and potentially led to stocking rates that exceeded the predator-prey balance (overstocking), at least in Lake Huron (Roseman and Riley, 2009; Johnson et al. 2010; He et al. 2015). As of Oct 2016 rising concerns of predator-prey imbalances in Lake Michigan (see: www.glf.org/pressrel/2016%20-%20LMC%20Predator%20Stocking.pdf) and Lake Ontario (see: www.glf.org/pressrel/2016%20-%20LOC%20stocking%20release.pdf) have led fisheries managers to reduce Chinook salmon and other piscivore stocking rates.

One major limitation to understanding contributions of naturalized populations to fisheries and their open water habitat use has been an inability to reliably identify and track fish from different sources. Given the current structure and mandates of management agencies in the Great Lakes (e.g., Ontario Ministry of Natural Resources,

Michigan Department of Natural Resources) broad scale monitoring of naturalized Chinook salmon populations at the spatial and temporal scales relevant to the fisheries are logistically and financially unfeasible. Analysis of natural markers of natal sources such as otolith microchemistry provides an alternative to traditional assessment programs such as numeration weirs and tagging studies. My previous research (Marklevitz et al. 2011) demonstrated the ability to use otolith microchemistry for identifying natal sources of Chinook salmon in Lake Huron, but questions remained about the accuracy of the technique including: “how do we accurate analysis of juvenile sections in adult otoliths?”, “is there temporal variability in the microchemical signals (e.g., Pangle et al. 2010)?”, and “how does temporal variability affect the ability to identifying natal sources?”. My comparison of the otolith microchemical concentrations and performance of four methodological approaches commonly found in the literature, demonstrated the importance of consistent analysis of otoliths within a study over a specific method choice (Chapter 3). This comparison also demonstrated that no method could produce temporally stable microchemical concentrations; illustrating the need to consider or compensate for temporal variability during study design and/or statistical analysis. Through comparisons of statistical methods for predicting natal sources, assessing natal source assignment accuracy and performing sensitivity analysis (Chapter 4) I demonstrated results and conclusions can be robust at spatial scales relevant to fisheries research and management; despite uncertainty in the otolith microchemical technique including temporal variability. This research furthers the use of otolith microchemistry through the application of the technique to predict natal sources of adult fish at a whole large lake (i.e., Great Lake) scale with comprehensive evaluation to ensure appropriate results and robust conclusions.

Using a combination of otolith microchemistry and hatchery markings (CWT and fin clips), I was able to identify origins of naturalized and hatchery Chinook salmon caught throughout Lake Huron (Chapter 4). There were significant contributions of fish from southern Georgian Bay rivers lake wide, dominant contributions from Michigan hatcheries to the Northern Main Basin fishery, and limited contributions of fish from central and southern Lake Huron rivers. I also found evidence of extensive incomplete mixing of fish from various natal regions in space and time (Chapter 4). This work forms the new basis of knowledge about Chinook salmon fisheries in the Great Lakes. It was the

first study to demonstrate regional variability in contribution from naturalized populations and hatcheries to the fisheries. It also dispelled the common assumption of completely mixed Chinook salmon fisheries in the Great Lakes (Adlerstein et al 2007, 2008; Connerton et al. 2009). Previously the only information available was from recaptures of coded wired tagged hatchery fish, primarily caught in US waters of Lakes Huron and Michigan (Adlerstein et al. 2007; 2008). These studies concluded that extensive movements of fish from different stocking locations support the completely mixed fishery assumption. My results indicate an angler (or assessment program) is much more likely to catch a Michigan hatchery fish in northern waters of Lake Huron than other areas of the lake. This particular example illustrates two critical points for sustainable management of the fishery. First, qualitatively, Michigan stocking programs likely have the greatest ecological effects in northern Lake Huron waters with the greatest impacts of alterations to stocking rates occurring in communities such as De Tour Village, Cheboygan, and Rogers City in Michigan and economies such as the small First Nations commercial fishery in northern Lake Huron. Second, quantitatively, estimates of survival, natural mortality, catchability and recruitment may be biased and hatchery to naturalized ratios inflated because most research and monitoring has occurred along the Michigan (US) coast. Minimal research or monitoring effort has occurred in the areas where most naturalized fish originate (Ontario coast and Georgian Bay) (Johnson et al. 2010). The Statistical-Catch-At-Age (SCAA) model (Brenden et al. 2012) that uses these parameters may therefore underestimate previous abundances of naturalized Chinook salmon in Lake Huron.

Examination of the spatial capture patterns of Chinook salmon using otolith microchemistry also demonstrated significant interbasin movement of fish from Georgian Bay into the Main Basin of Lake Huron (Chapter 4). Interbasin and interlake movement by fish has been identified as a key knowledge gap of fisheries research in the Great Lakes (Landsman et al. 2011). In Lake Huron, the movement by Georgian Bay origin fish specifically into Northern Main Basin is likely in response to prey abundances (Chapter 4). A major assumption in the SCAA model (Brenden et al. 2012) was no immigration or emigration into or out of the Main Basin. My results clearly demonstrated a significant violation to this assumption with 44% (2008) and 46% (2010) of fish in the lake wide

fishery originating from Georgian Bay. Violating the migration assumption may result in the SCAA overestimating naturalized recruitment from Main Basin tributaries while underestimating naturalized recruitment lake wide because most naturalized fish appear to originate outside of the Main Basin (i.e., Georgian Bay tributaries). Given the significant interbasin movement of Chinook salmon and incomplete mixing of the fishery, the spatial structure of the fishery should be factored into future analysis of population dynamics such as SCAA models.

Significant interbasin movement of Georgian Bay fish into the Main Basin also highlights the potential for migration of Lake Huron Chinook salmon into Lake Michigan to prey on more abundant alewife (Adlerstein et al. 2007, 2008; Williams 2012). Williams (2012) found increased proportion of naturalized, age 2+ Chinook salmon in Lake Michigan and hypothesized these could be emigrants from Lake Huron. Previous research has also documented Lake Huron stocked Chinook salmon captured in Lake Michigan but no captures of Lake Michigan stocked fish in Lake Huron (Adlerstein et al. 2007, 2008). The Lake Michigan fisheries are carefully managed through manipulation of stocking and harvest rates to match forage species abundances with energetic demands of predators (Eshenroder et al. 1995). Significant and unaccounted emigration of Lake Huron fish could compromise this balance in Lake Michigan. Building from my research, researchers at the Quantitative Fisheries Center at Michigan State University are currently (as of 2016) using otolith microchemistry to examine migration rates of Chinook salmon from Lake Huron into Lake Michigan. If migration proves to be significant, it would no longer be sufficient to manage Chinook salmon individually within each lake. Management of Chinook salmon fisheries in Lake Huron and Lake Michigan would need to be linked including coordination of assessment programs among state (US) and provincial (Canada) agencies to assess recruitment of naturalized fish in both lakes and determine migration rates between lakes.

One of the greatest concerns about the sustainability of Chinook salmon fisheries in the Great Lakes is competition with native lake trout (Crawford, 2001; Roseman and Riley, 2009). In particular, how to balance continued stocking in the presence of substantial naturalized reproduction without impeding restoration efforts for native lake trout. Throughout the Great Lakes, lake trout populations drastically declined through the

early 1900s but since 2000 increases in abundances, naturalized reproduction and naturalized recruitment are evidence of successful rehabilitation efforts (Muir et al. 2013). In Lake Huron, natural reproduction and catches of wild lake trout have increased since the late 1990s, especially in Northern Main Basin (Riley et al. 2007; He et al. 2012). The 2003 collapse of alewife in Lake Huron, partially attributed to Chinook salmon overstocking, has however elevated concerns of a prey limited situation and intensification of interspecific competition between Chinook salmon and lake trout (Dobiesz et al. 2005; Ebener, 2005; Roseman and Riley, 2009; He et al. 2015). The evidence I found of migrations by Chinook salmon originating around the Lake Huron Basin into northern Lake Huron supports concerns of intensive competition in this region. My results also demonstrate that Michigan hatchery fish potentially have the greatest effects of all the stocked fish on lake trout in Northern Main Basin. While ecologically it would first appear that reductions or complete cessation of Michigan stocking programs could alleviate some of this concern, my results also demonstrate such a management action would have disproportional consequences on the communities and economies relying on Northern Lake Huron fisheries. The extent of interspecific competition is also confounded by differences in ecological niches and the preferential consumption of alewife by Chinook salmon, which may aid restoration efforts by reducing consumption by lake trout (Diana, 1990; Miller and Holey, 1992; Eshenroder and Burnham-Curtis, 1999; Honeyfield et al. 2005; Fitzsimons et al. 2007; Jacobs et al. 2013). With the substantial declines of alewife abundances in all Great Lakes since the 1970s (O’Gorman et al. 2013), the complexities of Chinook salmon - lake trout - alewife interactions warrant further investigation and my research suggests northern Lake Huron would be a good place for such a study.

5.3 General conclusion

The introduction of Chinook salmon into the Great Lakes has provided ecological control of invasive forage fish and created valuable recreational fisheries, yet has also changed the food web and ecosystem. While the natural reproduction of naturalized Chinook salmon have long been known, assumptions about the need for indefinite stocking and a lack of information about naturalized recruitment, stock structure and

habitat use has potentially compromised the sustainability of the Chinook salmon fisheries. Much of the ecology of Chinook salmon in the Great Lakes remains unknown but my Ph.D. research has started to reveal aspects of their use of river and lake habitats, critical for sustainable management of the fisheries. The significant returns of hatchery fish and lack of reproductive isolation between hatchery and naturalized fish in the Sydenham River demonstrate a potential for stocking programs to affect the naturalized populations including reductions in productivity. Furthermore, extensive use of the accessible river by both naturalized and hatchery fish illustrate the potential of Chinook salmon regardless of origins to affect riverine ecosystems and river-resident fish species. My evaluation of the stock structure and habitat use of Chinook salmon in Lake Huron was the first in the Great Lakes to identify sources of naturalized fish and provide evidence of an incompletely mixed fishery. Incomplete mixing was contrary to the previous assumptions of a simple dynamic pool (completely mixed stock), used in fisheries management plans and for population dynamic models. My research also demonstrated significant interbasin movement which has implications for fisheries management in Lake Michigan in addition to Lake Huron. Incomplete mixing and interbasin movement are significant violations of current fisheries dynamic models (i.e., SCAA) which could lead to underestimation of naturalized recruitment. My research significantly improves our understanding of stock structure and habitat use of Chinook salmon in the Great Lakes, providing valuable information and consideration for future assessment of fishery dynamics and sustainable management of these purposely introduced non-native species.

5.3.1 Recommendations

- 1) In the Great Lakes, we need to better understand the ecology of naturalized Chinook salmon populations. With the reductions of stocking rates, Chinook salmon fisheries in the Great Lakes are becoming more reliant on naturalized reproduction. Broad scale monitoring of naturalized populations will likely continue to be logistically and financially unfeasible. Thus understanding how Chinook salmon have and are adapting to the Great Lakes environment and how environmental conditions affect recruitment of naturalized fish is going to be increasingly important to understanding and modelling the population dynamics and sustainably managing the fisheries.

- 2) We need further research on the effects of continued stocking on the naturalized populations in the Great Lakes. I found evidence of hatchery effects within a generation and no reproductive isolation between hatchery and naturalized fish. Previous studies have demonstrated potential for naturalized populations to have reduced productivity resulting from intensive and prolonged stocking programs. Such studies indicate that reduction in stocking rates may not result in predictable reductions of abundance, as naturalized recruitment could increase. Investigating the responses of naturalized populations as stocking rates decline will help with Great Lakes fisheries management but also provide valuable information to help design better stocking programs to restore native species (e.g., lake trout) and salmon populations in their native range.

- 3) We need to account for stock structure of the fisheries. Chinook salmon fisheries in the Great Lakes are not simple dynamic pools (i.e., completely mixed fisheries). There are varying contributions in the fisheries from naturalized and hatchery populations through space and time. Furthermore, there may be significant interbasin movement (e.g., Lake Huron to Lake Michigan, Lake Huron to Lake Erie, Georgian Bay to Main Basin Lake Huron). Based on similar migration patterns for defining a stock, my results demonstrate there are at least three stocks of Chinook salmon to consider in Lake Huron: 1) Northern Huron stock, dominated by State of Michigan hatchery fish and tend to remain in northern Lake Huron; 2) Georgian Bay stock, which migrates into and throughout the Main Basin, and; 3) South-Central stock, which is less prominent than the other two stock and migrate throughout the main basin. Spatial structure and the potential of migrations needs to be considered in fisheries management plans and quantified for incorporation into fisheries assessment models. Not accounting for these spatial structures of the fishery could result in underestimating naturalized reproduction and be putting the management of the predator-prey balance in the lakes at risk.

- 4) We should collect and archive otoliths and genetic tissue samples from juveniles and adult Chinook salmon for future analysis of stock structure and mixing. Otolith microchemistry and genetic analysis are powerful tools for stock delineation based on habitat use and population structuring, respectively. Both techniques continue to be developed and the analysis of each or a combination of these two natural markers will likely become more powerful and obtainable on the scales and in the timeframes needed for fisheries management in the future. The collection and archiving of otolith and genetic samples will enable future analysis of stock structure and potential changes as stocking rates change in the Great Lakes over time. Furthermore, refinement of methods could enable further research of evolutionary and ecological theory at finer spatial and temporal scales than those obtained in my research.

- 5) We need to improve tracking of individuals to better understand populations and their open water ecology. The Great Lakes provide a valuable system to study the ecology of salmon while foraging in open water. The spatial scale of the lakes and recent technological advancement such as the Great Lakes Acoustic Telemetry Observation System (GLATOS) (<http://data.glos.us/glatos>), make tracking individual fish for 2-5 yrs (the lifespan of a Chinook salmon) attainable. GLATOS is a network of acoustic receivers deployed throughout the Great Lakes Basin. The Great Lakes therefore represent a unique opportunity to study how individual-level processes translate into population level patterns. Tracking individuals from populations should allow for studies to determine population specific survival, natural mortality, catchability and recruitment rates in the fisheries. Tracking individuals should also allow for examination of spatial and temporal exposure to parasitism (i.e. sea lamprey), diseases (e.g. viral hemorrhagic septicemia) and the influence of prey abundances and environmental conditions on growth and survival. Finally, by examining individual level movement patterns and comparing among populations over time we should be able to evaluate the potential effects of heritability and environmental conditions (e.g. temperatures, currents, prey abundance) of open water migrations and habitat use.

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Appendices

Appendix A: Animal care protocol approval for research in Chapter 2 and 3



03.31.08
 *This is the 1st Renewal of this protocol
 *A Full Protocol submission will be required in 2011

Dear Dr. **Morbey**

Your Animal Use Protocol form entitled:

Chinook salmon stock composition in Lake Huron: using otolith microchemistry as a natural marker of stream origin

has been approved by the Animal Use Subcommittee.
 This approval is valid from **04.01.08 to 03.31.09**
 The protocol number for this project remains as **2007-043-05**

1. This number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this number.
3. If no number appears please contact this office when grant approval is received.
 If the application for funding is not successful and you wish to proceed with the project, request that an internal scientific peer review be performed by the Animal Use Subcommittee office.
4. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

ANIMALS APPROVED FOR 1 YEAR Highest Pain Level: B

Species	Other Detail	Housing/Use Locations	Animal # Total for 1 Year
Fish	Juvenile Chinook Salmon	Field Study	240
Fish	Adult Chinook Salmon	Field Study	

REQUIREMENTS/COMMENTS
 Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.

c.c. Approved Protocol - Y Morbey, J Wasylenko, D Cheshuk
 Approval Letter - J Wasylenko, D Cheshuk

The University of Western Ontario
 Animal Use Subcommittee / University Council on Animal Care
 Health Sciences Centre, • London, Ontario • CANADA – N6A 5C1
 PH: 519-661-2111 ext. 86770 • FL 519-661-2028 • www.uwo.ca / animal

Appendix B: Animal care protocol approval for research in Chapter 4

Animal Use Protocol Modification #6 | 7/26/2010
2008-077 Morbey

PI / PROTOCOL INFORMATION		
PI Name: Yolanda Morbey	Protocol Number: 2008-077	
Protocol Title: The evolutionary ecology of reproductive timing and senescence in Pacific salmon		
1. REQUESTED MODIFICATIONS TO PREVIOUSLY APPROVED ANIMAL USE PROTOCOL		
Identify all requested changes to the AUP identified above		
AUP Ref. #	Form Elements	
7, 8, 9, 10, 11, 13	Acute & Chronic Elements, PAU, Animal Groups Overview, Species Number, Source, Strains, Justification	C <input checked="" type="checkbox"/>
12, 21	Procedures Narrative, Categories of Invasiveness	D <input checked="" type="checkbox"/>
22	Protocol Personnel & Their Training Requirements	H <input checked="" type="checkbox"/>
App. 6	Field / Wildlife Research	6 <input checked="" type="checkbox"/>
2. PROVIDE JUSTIFICATION FOR PROPOSED CHANGES OUTLINED IN THIS PROTOCOL MODIFICATION		
In fall 2010, a different species (Chinook salmon) will be used instead of kokanee because logistical constraints associated with working at our remote field site in southern British Columbia make it impossible to work there this year. Instead, we propose to work on Chinook salmon in southern Ontario. We have also added some new procedures (fat meter reading and recapture of naturally-moribund [dying] fish) and will be using a different type of external tag.		
3. PROCEDURAL CONSEQUENCES – See Section 20, AUP Reference		
1. From BOTH the Project OVERVIEW & DETAIL perspectives, identify and describe specific procedural or other elements (eg. drugs, chemicals, agents, materials and devices) associated with this revised Animal Use Protocol that may produce Pain, Distress or Impairment and identify all possible consequences (Behavioural, Physical, Biochemical, Physiological and Reproductive) for this species.	PROJECT OVERVIEW: Changes are proposed for the Approach/Research Plan for implementing Objective 1 (testing hypotheses related to the behavioural and physiological mechanisms underlying individual variation in reproductive lifespan), because we will be working on a different species in the 2010 field season. Field studies will be now beconducted on spawning Chinook salmon from the Sydenham River (near Owen Sound, Ontario). PROJECT DETAIL: There will be some modification to Experimental Group #3 (2008-077 Morbey 04.27.09 MAJMOD). In	

2008-077 Morbey MOD #6 07.15.10 APPROVED.doc
Page 1 of 7

Curriculum Vitae

Name: Stephen A.C. Marklevitz

Post-secondary Education and Degrees:

Dalhousie University
Halifax, Nova Scotia, Canada
2002- 2007, B.Sc. (Marine Biology and Oceanography)

Western University,
London, Ontario
2007- 2009, M.Sc. Biology (Environment and Sustainability)

Western University,
London, Ontario
2012- 2014, Certificate in University Teaching

Western University,
London, Ontario
2009- 2017, Ph.D. Biology (Environment and Sustainability)

Honours and Awards:

Natural Science and Engineering Council Post Graduate
Scholarship (NSERC PGS D)
2009-2012

Ontario Graduate Scholarship
2012

Queen Elizabeth II Ontario Graduate Scholarship in Science and
Technology (declined)
2012

OFAH/Toronto Sportsmen Fisheries Research Grant
2012

Faculty of Science Graduate Student Teaching Award
2012

Community of Practice in Ecosystem Health- Canada Graduate
Training Award
2009

Environment & Sustainability Graduate Student Award of
Excellence
2008-09, 2009-10, 2010-11, 2012-13

PSAC Local 610 Academic Achievement Scholarship
2013

Clemens-Rigler Graduate Student Travel Fund
2010

IAGLR-OMNR Student Travel Award
2009, 2012

Environment & Sustainability Graduate Student Travel Award
2011

Department of Biology Graduate Student Travel Award
2011

**Related Work
Experience**

Aquatic Ecosystem Biologist
Lake Erie Management Unit
Ontario Ministry of Natural Resources and Forestry
2014- present

Teaching Assistant
Centre for Environment and Sustainability
Western University
2011-2013

Teaching Assistant
Department of Biology
Western University
2007-2010, 2013

Contract Biologist
Bedford Institute of Oceanography
Fisheries and Oceans Canada
2005-2007

Publications:

Marklevitz, S.A.C., Morbey, Y.E., 2017. Habitat use and arrival timing of hatchery and naturalized Chinook salmon (*Oncorhynchus tshawytscha*) population spawning in a Great Lakes tributary. Transactions of the American Fisheries Society. IN PRESS

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