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Introduced Chinook salmon (*Oncorhynchus tshawytscha*) in Lake Huron: do they spawn at the right time?

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A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science
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INTRODUCED CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) IN
LAKE HURON: DO THEY SPAWN AT THE RIGHT TIME?

(Spine title: Reproductive timing of Lake Huron Chinook salmon)

(Thesis format: Monograph)

by

Meghan Teresa Gerson

Graduate Program in Biology

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

The School of Graduate and Postdoctoral Studies
The University of Western Ontario
London, Ontario, Canada

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THE UNIVERSITY OF WESTERN ONTARIO
SCHOOL OF GRADUATE AND POSTDOCTORAL STUDIES

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Lake Huron: do they spawn at the right time?**

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Abstract

Chinook salmon (*Oncorhynchus tshawytscha*), following their introduction to the Great Lakes, have successfully colonized many tributaries. Under the hypothesis that colonization success is facilitated by intrinsic factors (i.e., preadaptation), I predicted that patterns of reproductive timing in an introduced population would show similarities with those in their native range. To test this prediction, attributes of reproductive timing were characterized in Chinook salmon from the Sydenham River, Ontario. In their native range, female Chinook salmon exhibit a seasonal decline in reproductive lifespan, a decline in fat stores, low egg retention at death ($< 0.5\%$), and spawning at temperatures below 12.8°C . In contrast, Sydenham River Chinook salmon showed no seasonal decline in reproductive lifespan or fat stores and nineteen of twenty females had egg retention $\geq 0.5\%$. Also, many individuals (30%) spawned when water temperatures exceeded 12.8°C . Thus, individuals do not appear to be pre-adapted in this system.

Keywords: Chinook salmon, reproductive timing, spawning, adaptation, migratory cues

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Introduction

Pacific salmon life history

Pacific salmon of the genus *Oncorhynchus* are a group of fishes native to the North Pacific Ocean (Groot and Margolis 1991). There are seven species of Pacific salmon: *Oncorhynchus nerka* (sockeye salmon), *O. gorbuscha* (pink salmon), *O. keta* (chum salmon), *O. tshawytscha* (Chinook salmon), and *O. kisutch* (coho salmon) comprise the five species that are found in North America. The remaining two species, *O. masou* (masu salmon) and *O. rhodurus* (amago salmon) can only be found in Asia (Kato 1991). This group can be broadly characterized by being semelparous (die after breeding) and anadromous (migrate from salt water to spawn in freshwater). Life history characteristics such as age at maturity, length of freshwater residence, and migration and spawning timing vary extensively among and within populations of the same species (Willson 1997).

Chinook salmon populations in North America can be found from Kotzebue Sound, Alaska, south to Central California (reviewed in Healey 1991). Similar to other Pacific salmon, Chinook salmon are anadromous, semelparous and display a wide range of life history variation throughout their range. The majority of this variation stems from two distinct eco-types defined by the time spent in freshwater at different life history stages. Stream-type Chinook salmon spend longer periods of time in freshwater as juveniles before they migrate out to the ocean and adults return to freshwater spawning habitat in the spring months before spawning. Juvenile Chinook salmon of the ocean-type migrate to the ocean earlier than those of the stream-type and adults return between late summer and late fall to spawn shortly after reaching spawning habitat (Healey 1983).

Chinook salmon reach maturity between the ages of 2 and 6 years, with the majority of variation in age occurring between eco-types (Healey 1991).

Once mature, Chinook salmon migrate back to their natal waters to spawn. Like other Pacific salmon, Chinook salmon are capital breeders and cease feeding prior to migrating to spawning areas (Fleming and Reynolds 2004). They must rely on somatic energy stores (fat and lean tissue) to sustain migration and subsequent spawning activities. Migration distance differs greatly among populations, ranging from only few kilometers to over 3,000 kilometers for populations that spawn within the Yukon river system of Alaska (Healey 1991). The timing of migration and spawning varies widely among populations but is consistent among years, leading to run timing being commonly used to differentiate populations (Waples et al. 2001).

When a female prepares to spawn (the act of depositing eggs) she will first dig a redd (nest) and over the course of a few days will repeatedly spawn with a male until all or most of her eggs have been deposited and buried in the gravel of the stream bed. Chinook salmon females can produce as few as 2,000 eggs or as many as 17,000 eggs and fecundity (total number of eggs in body cavity) is typically correlated with size (Healey and Heard 1984). Typical egg retention (eggs remaining in the body cavity as counted after death) for Chinook salmon females is around 0.5% of fecundity (Hruska et al. 2011).

After spawning, females remain to guard redds from later-nesting females that attempt to reuse high quality nest sites while males seek out additional breeding opportunities. The duration of female defense of a redd varies (6-25 days) among and within populations and often shows a seasonal decline (Hendry et al. 2004). Eggs in the

gravel incubate until the following spring when they emerge as alevins. Emergence occurs between February and May with earlier emergence occurring in more southerly populations (Healey 1991). Alevins will remain in freshwater feeding off their yolk sac for several weeks and once they begin feeding they are referred to as fry. Before fry migrate out to the ocean they take up residence in freshwater for a period of time ranging from a few weeks to up to a year or more (Healey 1983). During freshwater residence, fry set up territories for feeding (reviewed in Healey 1991).

Temperature effects on reproduction

A literature review conducted by the United States Environmental Protection Agency (McCullough 1999) reported typical temperatures for Chinook salmon spawning activities. Chinook salmon in the Columbia river system typically spawn at temperatures between 5.6 - 12.8°C (McCullough 1999). While this review only included Chinook salmon in the Columbia river, these temperatures are consistent with those experienced elsewhere in their range (Quinn et al. 2002). When spawning within typical temperatures, Chinook salmon can perform normal behaviours and undergo metabolic processes without experiencing any thermal stress symptoms (Sullivan et al. 2000). High water temperatures can negatively impact Pacific salmon, and elevated water temperatures seem to be the cause of recent losses of migrating sockeye salmon in the Pacific Northwest (Mathes et al. 2010). In addition, high water temperatures have been blamed for increased egg retention (Quinn et al. 2007), increased susceptibility to disease (Wagner et al. 2005), and decreased reproductive lifespan (Morbey and Ydenberg 2003).

Reproductive timing: adaptation

The timing of migration, arrival at spawning grounds and spawning are key life history traits in semelparous salmonid species (Fleming 1998). Migration and spawning timing variation among populations is believed to have evolved in response to water temperature and flow during both adult migration to the breeding grounds (Quinn and Adams 1996; Jonsson and Jonsson 2009) as well as during juvenile emergence (Beacham and Murray 1987; Webb and McLay 1996). While migration and spawning timing tend to vary considerably among populations (Hodgson and Quinn 2002), among years, reproductive timing of a given population is highly predictable (Waples et al. 2001). This is partly because the timing of freshwater entry and spawning are highly heritable ($h^2 = 0.2 - 0.4$) in salmonid populations (Smoker et al. 1998; Stewart et al. 2002; Keefer et al. 2004).

It is widely acknowledged that changes in photoperiod trigger initial reproductive maturation while adults are still in the ocean (Clarke et al. 1994; Quinn and Adams 1996). Freshwater entry and subsequent migration to the spawning habitat is generally assumed to be triggered by other environmental cues (e.g., water temperature and flow) that correlate with optimal conditions on natal spawning grounds (Jonsson and Jonsson 2009). Since there is variation in migration timing among populations within river systems that experience similar temperature and flow regimes, populations have evolved different responses to the same cues (Hinch et al. 2006). Responses to cues may vary among and within populations because of variability in migration distance, energy demands for migration, and river temperature (Hinch et al. 2006).

Within populations, successful spawning by females depends upon when individuals arrive to the spawning grounds in relation to other arriving females (Morbey and Ydenberg 2003). During breeding, early arrival to spawning habitat allows females to obtain the highest quality territories. However, early-arriving females must defend their nests longer after spawning to prevent re-use of their nest by later arriving females (Morbey and Ydenberg 2003). Alternatively, later arriving females evolve shorter reproductive lifespans because fewer females will arrive later and reuse nests. Instead, these females invest more energy in gonads than somatic stores (Hendry et al. 1999). This causes the timing of nest defense to vary within salmonid populations due to selection imposed by nest site re-use. Nest re-use appears to be an important selective factor on reproductive timing in many salmon populations (Hendry and Day 2005). Reproductive timing has also been shown to evolve rapidly among many taxa in response to the seasonal shifts associated with climate change (Bradshaw and Holzapfel 2006).

Reproductive timing: plasticity

In addition to local adaptation to prevailing temperature and flow regimes, Pacific salmon exhibit a high degree of phenotypic plasticity that facilitates immediate changes in reproductive timing (arrival timing and reproductive lifespan) in response to changes within a season (Crozier et al. 2008; Jonsson and Jonsson 2009). For example, in fall-spawning Chinook salmon near Puget Sound, WA, individuals that were moved from the Soos Creek population (mean Sept temperature $\sim 11^{\circ}\text{C}$) to an area of warmer water (mean Sept temperature $\sim 19^{\circ}\text{C}$), to found the University of Washington Hatchery population, had a shift to later spawning in just one generation indicating that timing of

spawning is plastic in response to the prevailing temperature (Quinn et al. 2002). Increases in water temperature also led to earlier and later shifts in migration timing in a population of Chinook salmon in the Columbia River in order for individuals to avoid the highest temperatures (Gonia et al. 2006). However, since there is a genetic component of spawning timing in Pacific salmonid populations (Smoker et al. 1998; Stewart et al. 2002; Keefer et al. 2004), consistent seasonal temperature increases could be shifting spawning runs to later in the fall when temperatures are cooler (Quinn and Adams 1996).

Salmonid introductions

Due to their high value as a food and sport fish, Pacific salmon have been introduced to numerous new environments worldwide (Lever 1996). While introductions have been frequent, those resulting in successful establishment are few (Mills et al. 1993; Crawford and Muir 2008). Unsuccessful introductions are typically due to selecting a mismatched genetic strain for the new environment (Salmenkova 2008). However, when salmonid introductions are successful and large populations experience new environments, traits will diverge rapidly in response to new selective pressures (Stockwell et al. 2003; Stearns and Hendry 2004).

Chinook salmon were taken from their native range and introduced to New Zealand and Southern Patagonia in the early 20th century, and to the Great Lakes in the 1960s. Populations of reproducing Chinook salmon colonized new locations rapidly in all these cases (Becker et al. 2007). Migration and spawning timing are two life history traits that are likely to respond rapidly to selection, and populations of introduced

salmonids have been used to test for the divergence of these traits (Quinn et al. 2000; Kinnison et al. 2001; Kinnison et al. 2003).

Documentation of altered reproductive timing in response to new environmental seasonality is widespread (Gharrett and Thomason 1987; Quinn et al. 2000; Quinn et al. 2001; Quinn et al. 2011). Evidence of introduced salmon populations adapting to new local environments has been observed after as few as 9 -13 generations (Gharrett and Thomason 1987; Hendry et al. 1998; Hendry 2001). Extensive studies on introduced New Zealand Chinook salmon revealed rapid genetic divergence of multiple traits in response to different selective pressures since their recent colonization in the early 20th century. For example, a trade-off in reproductive investment by females (Kinnison et al. 2001) and divergence in physical characteristics of males (Kinnison et al. 2003) was found in response to migratory distance. Females that migrated further had a higher ratio of egg number to egg size (Kinnison et al. 2001) and males that went a similar distance showed reduced size in secondary sexual characteristics (hump height and snout size) (Kinnison et al. 2003). In response to temperature, Chinook salmon populations that spawned in warmer water returned and matured later than those populations that spawned in colder water (Quinn et al. 2000). Most recently, genetic divergence in spawning date (18 days later) was found in response to new environmental seasonality (Quinn et al. 2011).

Pre-adaptation

Chinook salmon were introduced into rivers in Patagonia beginning in the early 20th century and rapidly established anadromous populations in the Pacific and more

recently Atlantic river basins (Ciancio et al. 2005). In general, establishment of anadromous populations is less frequent than establishment of resident freshwater populations (Pascual and Ciancio 2007). The success of Chinook salmon in Patagonia suggests that they may have already possessed adaptations allowing them to survive and reproduce in this novel environment (Ciancio et al. 2005). This phenomenon is known as pre-adaptation. In other words, traits that Chinook salmon populations evolved in native environments could facilitate success in new environments. Pre-adaptation is a common theme in biological invasive plant literature (Jenkins and Keller 2011) and has been recently described as a critical component of establishment success of introduced amphibians to new environments (Tingley et al. 2011). Chinook salmon populations exhibit a wide array of life history tactics (e.g., timing) that are highly plastic in response to environmental conditions, suggesting that pre-adaptation is possible in facilitating colonization of novel environments.

Chinook salmon in Lake Huron

The near extirpation of native Lake Trout (*Salvelinus namaycush*) in Lake Huron led to an increase in prey fish such as invasive alewives (*Alosa pseudoharengus*). In order to manage the problem levels of prey fish, Chinook salmon (*Oncorhynchus tshawytscha*) were introduced in the late 1960s. Chinook salmon of the ocean-ecotype, from Puget Sound (Green River, WA, U.S.A.) were first successfully introduced into Michigan waters of Lake Huron beginning in 1968 and spread to Ontario waters soon thereafter (Weeder et al. 2005; Johnson et al. 2010). This introduction proved successful not only for reducing alewife numbers but in stimulating recreational fisheries in the

Great Lakes (Kocik and Jones 1999). Chinook salmon in the Great Lakes are believed to have similar life histories as their Puget Sound relatives. However, having no access to salt water makes them adfluvial migrants (fish that live in lakes and migrate to rivers to spawn). Evidence of naturally reproducing Chinook salmon was first found in tributaries of Lake Huron in the mid 1980s (reviewed in Crawford 2001). Adults typically spawn between late September through October and fry emerge from the gravel in May and remain in streams until late May or June when they migrate to the open lake (Kocik and Jones 1999).

Natural reproduction of Chinook salmon now occurs in at least 17 different Lake Huron tributaries (Marklevitz et al. 2011) and populations could now persist through natural reproduction alone (Johnson et al. 2010). The Chinook salmon of Lake Huron were important in controlling numbers of invasive prey fish, but recent declines of prey fish could be impacting growth and size of the large predatory fish population of the lake (Dobiesz et al. 2005). Recent evidence also indicates that genetic divergence of Lake Huron Chinook salmon has occurred in less than 10 generations due to founder effects and genetic drift in small populations (Suk et al. 2011).

Using terms defined by Gross (1998) the Chinook salmon of Lake Huron are exotic (not native to the Great Lakes) and naturally reproducing (natural reproduction can sustain the population) with some supplementation. Approximately 3.5 million Chinook salmon fry (age 0) are added in the spring each year throughout Ontario and Michigan waters (Johnson et al. 2010). These fry are raised in local hatcheries run by local sportsmen clubs. The gametes are taken primarily from the Mill Dam in Owen Sound, Ontario, located on the Sydenham River. In the Great Lakes, river systems that include

both hatchery-reared and wild spawning Pacific salmon are common in areas where fish are supplemented to sustain populations. In effort to sustain natural populations of Pacific salmon, well-managed supplementation programs aspire to maintain the characteristics of native populations (Brannon et al. 2004). In other systems, differences between hatchery-reared versus wild origin fish have been shown in size (Swain et al. 1991) and competitive behaviour (Metcalf et al. 2003). However, hatcheries that are originally established from gametes collected from the local population can result in hatchery-reared and wild individuals with similar reproductive traits (Schroder et al. 2008) and overall reproductive success (McGinnity et al. 2004).

Objectives and hypotheses

Chinook salmon have been reproducing naturally in Lake Huron tributaries for 10 generations and wild adults make up a majority of the lake wide population. However, information is lacking on reproductive success of Chinook salmon in their spawning habitat. The overall objective of this thesis is to determine whether Chinook salmon in Lake Huron are pre-adapted to spawn at times within temperatures typically experienced in their native range. Under the hypothesis that Lake Huron Chinook salmon are pre-adapted to local conditions, spawning timing and measures of reproductive lifespan should be similar to what is typical of Chinook salmon in their native range. I predicted that females should have a seasonal decline in reproductive lifespan and corresponding decline in fat stores, as occurs in the ancestral population. In addition, I predicted that egg retention by females after spawning should be typical for Chinook salmon in their native range and that spawning should occur within temperatures typical for Chinook

salmon in their native range. Since temperatures are likely to decline throughout the fall spawning season as the onset of winter approaches, I predicted there would be a negative effect of high temperature on egg retention. Females that spawn earlier in the season under higher temperatures should retain a greater number of eggs than females that spawn later in the season. Since differences in size have been found between hatchery-reared and wild populations (Swain et al. 1991), I predicted that hatchery-reared fish should be larger than wild female Chinook salmon, which may cause differences in reproductive traits between hatchery-reared and wild fish.

Methods

Study site

The Sydenham River, located in Grey County in southern Ontario, drains into Lake Huron at Owen Sound (Figure 1). This river is stocked yearly with Chinook salmon fry that are raised in a private hatchery facility run by the local sporting and fishing club, the Sydenham Sportsman's Association (SSA). The SSA collects gametes at the Owen Sound Mill Dam (Figure 1) from both wild and hatchery-reared fish. The gametes are then taken back to their private hatchery facility where they are fertilized and raised until they reach the appropriate size for release (e.g., the following spring). Technicians from the Ontario Ministry of Natural Resources clip the adipose fin of most fish approximately ten days before the release of all hatchery-reared fish. Since Chinook salmon exhibit natal homing and return to their place of birth to spawn (Healey 1991), fry are released along a section of the Sydenham River where natural reproduction is known to occur.

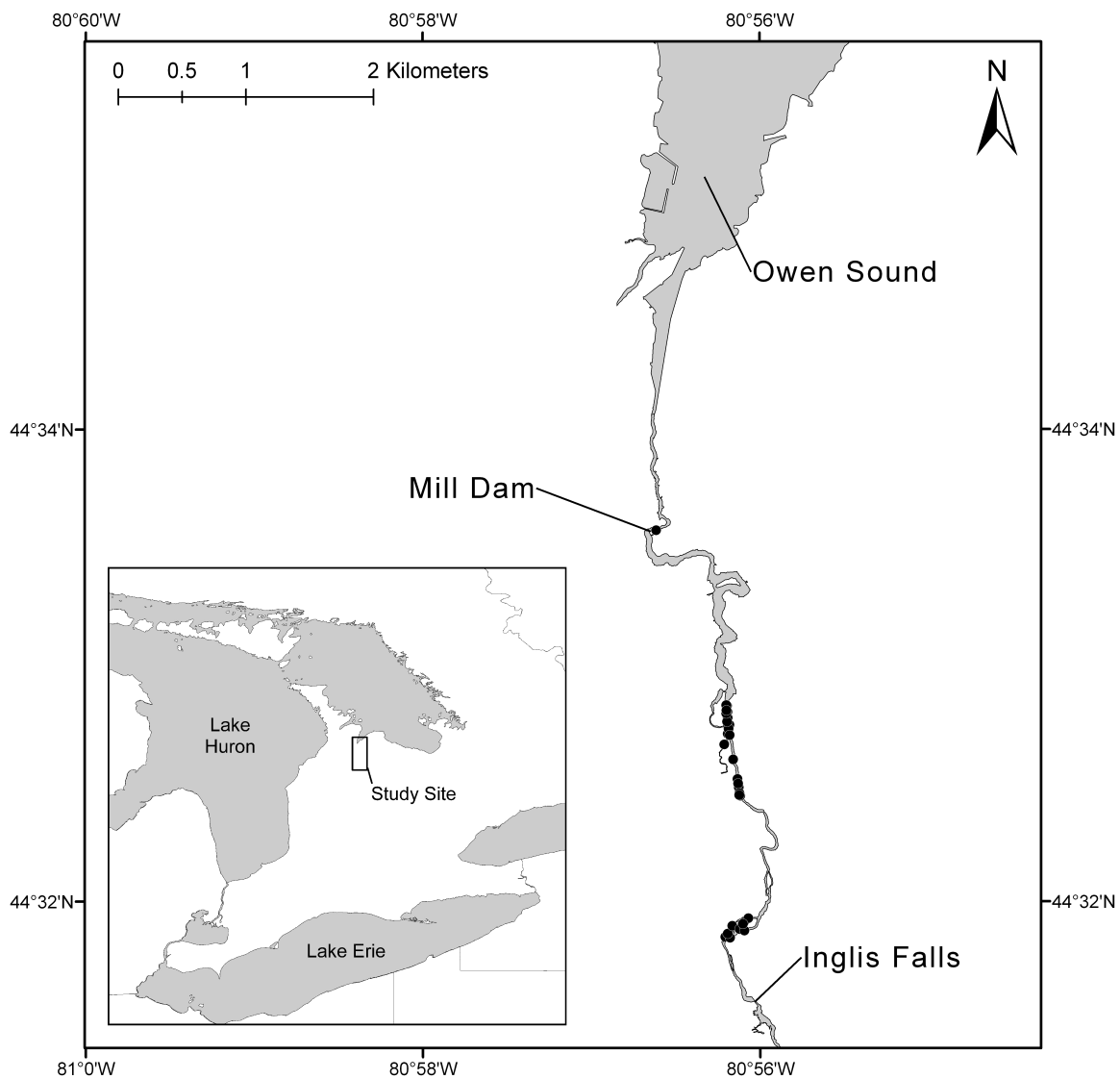


Figure 1. Location of the Sydenham River in Southwestern Ontario. Spawning locations are indicated by the black dots. Female Chinook salmon were tagged at arrival to the Mill Dam and are blocked from going further upstream by Inglis Falls.

The Owen Sound Mill Dam is located approximately 1 km from the mouth of the Sydenham River and controls recreational water levels on the Sydenham River as it passes through the city of Owen Sound. It contains the first fish ladder ever constructed in Ontario that allows for the passage of fish. The ladder contains wooden boards within each section that can be added or removed to either decrease or increase the flow of water to aid fish in swimming up the ladder. In the uppermost and largest section of the fish ladder a trap can be deployed, which can be used to capture fish for sampling. A steel basket (approximately 1 m³) can be hydraulically lowered into this section. When completely lowered the basket sits entirely below the water level. Therefore, when the fish swim up the ladder they eventually jump into the uppermost section and into the basket. When the trap is fully deployed, a section of aluminum bars are placed just above the basket and prevent fish from jumping out. Once the basket has fish, it can then be hydraulically raised to allow easier access to the captured fish for sampling. The length of river accessible to fish upstream from the dam is 6 kilometers; fish are blocked from going further upstream by Inglis Falls.

There are two main areas of suitable spawning habitat downstream of Inglis Falls on the Sydenham River (Figure 1). The majority of Lake Huron Chinook salmon spawn in these two main areas from late September through October. The first is located along Harrison Park and the second is a series of artificial spawning channels (2 km in length), created and maintained by the SSA. These two areas have streambeds composed of small stones and gravel, which are more suitable for spawning, than the bedrock that comprises the majority of the natural streambed.

Temperature

To determine mean temperature along the length of the river accessible to spawning fish, temperature sensors were placed throughout the river for the period 2 Sept – 24 Oct 2010. This section of the Sydenham River has not been historically monitored for temperature, so a total of eleven temperature sensors were deployed to assess whether there were variations in temperature along the river. The first temperature sensor was placed at the dam and each subsequent temperature sensor was approximately 50 – 500 m upstream ending 50 m above the spawning channels. Temperature was recorded every fifteen minutes. Three of the temperature sensors were not used because they became dislodged and did not record water temperature accurately. An Environment Canada gauging station (02FB007), located in the Sydenham River upstream of the falls (44°31'N, 80°55' W), has been recording daily discharge rates since 1980. These public data were downloaded from the Environment Canada website¹. Water temperature has also been measured at 15-minute intervals at this location since 2009 (Grey Sauble Conservation Authority, unpublished data).

An ANOVA was performed to determine whether mean water temperature from the eight temperature sensors were not significantly different. The mean daily temperature of the Sydenham River was then calculated from the mean daily temperature averaged across all eight temperature sensors for each day of the spawning season. To determine if 2010 was a typical or atypical year, regarding temperature, linear regression was used to relate the daily mean temperature of the spawning areas and the daily

¹<http://www.wateroffice.ec.gc.ca>

temperature collected at the Environment Canada gauging station. Water discharge, but not temperature, has been historically measured at this location. Since water discharge can be correlated with temperature, the temperature collected at the Environment Canada gauging station was then related to the daily discharge measured at the same location in order to examine historical temperature trends.

Estimation of a fecundity vs. fork length relationship

Linear regression of fecundity on fork length is frequently used in salmon research to obtain fecundity estimates without killing fish (Beacham and Murray 1993; Dickerson et al. 2005; Anderson et al. 2010). To obtain an estimate of average fecundity for this population, female Chinook salmon ($n = 30$) were sampled from fish caught in the Owen Sound Salmon Spectacular Fishing Derby. This annual fishing derby is organized by the SSA and took place between 27 Aug and Sep 5 2010. To be eligible for a prize, fish caught must be weighed and measured at an official weigh station. An Ontario Ministry of Natural Resources technician is on hand at each station to gather lengths and weights. The culmination of this event is an annual fish fry from donated catch. All females sampled for lengths and fecundities were obtained from these donated fish. All females donated between 1 Sep and 5 Sep 2010 were measured for fork length (cm; tip of snout to the fork of tail) and weight (kg; weight of the whole fish). Fecundity (egg count) was determined by first weighing both ovaries and a subsample of approximately 50 eggs. The eggs in the subsample were then counted. These values were then used to estimate fecundity using Equation 1.

$$fecundity = [(total\ ovary\ weight)(eggs\ in\ subsample)] / (subsample\ weight) \quad (1)$$

The data collected from derby-sampled fish were combined with existing fork length and fecundity data for Chinook salmon in Lake Huron collected by the Ontario Ministry of Natural Resources (OMNR, unpublished data). To obtain an equation relating fecundity to fork length, a least-squares linear regression between fecundity and fork length was then performed using R version 2.10.1.

Population sampling

Female Lake Huron Chinook salmon were sampled daily from 13 Sept – 13 Oct 2010. During this time both male and female fish were tagged; however, only females were used in this study. During the beginning of the season the trap was set overnight and all fish in the trap were tagged. Upon completion of tagging all fish in the trap it was re-deployed for a period of 3 to 4 hours and any fish in the trap were tagged in the afternoon. During the peak of the run, the trap was not set overnight since large numbers (up to 50) of fish could be confined for long periods of time, which caused added stress when individuals attempted to jump from the trap. During the peak of the run the trap was deployed (~ 7:00 am) until the trap contained approximately 20 fish (i.e., the maximum number we handled in one day). There was a gap in sampling from 3-8 Oct while the SSA was doing their annual gamete collection.

Fish were removed from the trap and were immediately anaesthetized using a mixture of clove oil (2.6 ml) and ethanol (~100 ml) that was mixed vigorously in a large cooler filled with water (90 L). At this clove oil concentration (25 mg/L) fish were anaesthetized in less than three minutes and could recover in less than five minutes once exposed to fresh water (Taylor and Roberts 1999). While anaesthetized, fish were

tagged at the base of the dorsal fin with a 3 cm, brightly coloured Peterson Disc tag (Floy Tag Co., Seattle, WA). To apply tags a 5” nickel pin was inserted through one Peterson Disc and pushed through the dorsal rays at the base of the dorsal fin. A second Peterson Disc was then placed on the opposite side of the fish and the pin was then bent and twisted, using needle-nose pliers, in a knot to lie flat against the side of the fish. These tags have been used in many studies examining reproductive behaviour of spawning salmon (Quinn and Foote 1994; McPhee and Quinn 1998; Hendry et al. 1999). Each tag had an individual, highly visible, two-letter code that was written in permanent marker. All fish were also tagged with a passive integrated transponder (P.I.T.) tag that was used for another study. These tags were inserted into the body cavity through a small incision (~2 mm) that was then closed using a few drops of Vet Bond® skin adhesive. Individual Chinook salmon were measured (fork length), weighed and females checked for ripeness (reproductive condition) by gently squeezing the abdomen of the fish. Fish were categorized as ripe if eggs were ejected from vent upon squeezing.

A relative measure of somatic energy stores (fat percent) was estimated using a handheld Distell Fish Fatmeter (Distell Inc., West Lothian, Scotland). This handheld unit contains a microwave oscillator that emits a low-powered wave (frequency, 2 Ghz ± 2,000 Mhz; power, 2mW) that interacts with the water contained in the body tissue at the sampling location. The sensors in the device convert the water concentration to an estimate of lipid concentration in the body of the fish. The meter is pre-programmed with a specific calibration function for estimating somatic lipids in Chinook salmon. Manufacturers recommend taking eight total readings, four on each side of the fish. The readings are then averaged to determine the average percentage of fat within the

individual. A recent study has found that as little as 2 readings on one side of the fish can be just as accurate in estimating percent fat (Crossin and Hinch 2005), even in spawning salmon which tend to have much lower levels of fat (Hendry and Beall 2004). Therefore, I took three readings taken above the lateral line on the left side of the fish and this significantly decreased handling time. Analyses used the mean of these three readings. Origin (hatchery-reared or wild) was determined for each fish by scanning for the presence or absence of an adipose fin. After sampling, fish were allowed to recover and were then released back into the river directly upstream of the dam.

Fecundity of tagged females was estimated using the predictive model for fecundity. Mean reproductive lifespan and days on nest were determined from the 30 females observed spawning. A Kolmogorov-Smirnov one-sample test, suitable for testing for differences between cumulative frequency distributions (Zar 1984), was performed to determine any difference in the arrival schedule between hatchery-reared and wild fish.

Daily observations

The two main spawning areas were surveyed daily for tagged females. The terrain along the riverbank between these two areas was rough and difficult to hike and the spawning habitat was poor (e.g., bedrock substrate), therefore it was only walked weekly to check for spawning fish. Female Chinook salmon were surveyed from the riverbank using binoculars while wearing polarized sunglasses. Upon locating a fish, a 2-minute behavioural observation was made. Location of the fish (UTM coordinates obtained using GPS), behavioural status (settled or moving), and paired status (settled in one

location with a male; yes or no) was recorded. Additional breeding behaviours including digging (female actively moving gravel to prepare nest), defense (aggressive behaviour towards other females in area), and spawning (the act of a female and male releasing eggs and milt simultaneously) were also recorded. Nesting females were typically settled (stationary in one location during entire 2 minute observation) paired with a male, and exhibited defensive behaviours. Based on these behavioural data as well as arrival day (day female was tagged), I determined each female's settle day (day first seen settled on a nest), day of death (day last seen alive), reproductive lifespan (difference between day of death and arrival day) and days on nest (difference between day of death and settle day). All formerly occupied nests were also observed daily to infer nest success by determining nest site re-use. These nests were recorded as either re-used (scored as 0) or not reused (scored as 1) by later arriving females. Based on observations of spatial distribution of spawning pairs in the Sydenham River, nests were considered re-used if there was a settled female within 3 m² of the original female's nesting location.

To determine if females showed a typical seasonal decline in reproductive lifespan and a corresponding decline in fat stores, linear regressions were used to determine the relationships between reproductive lifespan and arrival day, and percent fat at arrival and arrival day. A linear regression between reproductive lifespan and percent fat at arrival was also performed to determine whether fat measured at arrival could be used to predict how long a female would live.

Mean daily temperature of the river was used to calculate the mean temperature experienced for individuals throughout their reproductive lifespan and while settled on a nest. To determine if females in the Sydenham River experienced higher temperatures

than typically experienced in their native range, a Pearson's chi-square test was used to compare observed temperature experienced throughout reproductive lifespan to that expected of females in their native range (zero females should spawn above 12.8° C) as described by McCullough (1999). A two-sample t-test was used to determine if mean temperature experienced while spawning differed between hatchery-reared and wild fish.

A backwards stepwise multiple linear regression was used to identify the important factors influencing reproductive lifespan and number of days on a nest. The original models included fork length, percent fat at arrival, temperature and origin as independent variables and the interactions between the covariate of origin and fork length as well as origin and fat. Non-significant interaction terms of the highest order were dropped from the model followed by sequentially dropping the non-significant factors until only significant factors remained.

Similar to Hendry et al. (2004), multiple logistic regressions were used to estimate selection on reproductive traits (arrival day, settled day, reproductive lifespan and days on nest) imposed by nest site re-use. To test for selection, two backwards stepwise multiple logistic regressions were run, each including two reproductive traits. The first included arrival day and reproductive lifespan and the second included breeding day and days on nest. Also included in each model were fork length and origin as independent variables and the interactions between origin and all independent variables. Non-significant interaction terms were sequentially dropped from the saturated model followed by non-significant factors until only significant factors remained. In order to standardize the logistic coefficients and their standard errors to make them comparable to

other published studies, these values were multiplied by the standard deviations of the original factors (Lande and Arnold 1983; Janzen and Stern 1998).

Egg retention

Many of the tagged females died and then were washed downstream to unknown locations or were scavenged before they could be sampled. Therefore, all dead females that were found on the riverbank within 1 day of death ($n = 20$) were dissected to determine egg retention (percent of eggs not released through spawning). If fewer than 100 eggs remained, eggs were counted individually. If greater than 100 eggs remained; all eggs were weighed in a Whirlpack® sample bag attached to a 10 g Pesola® scale followed by a subsample of a known number of eggs (~ 30) weighed in a similar fashion. These values were then used to estimate the total number of eggs remaining. To determine egg retention of tagged females, their fecundity was estimated from the fecundity-length relationship. The percentage of eggs retained for untagged individuals was determined using the average fecundity for this population (5504 eggs). The lengths of untagged fish were not recorded since after spawning the tail of females could be damaged from digging and would not represent the same measurement as fish tagged at the dam.

Females were categorized as either completely spawned or not, following Hruska et al. (2011). Since it is common for a few eggs to remain trapped in the body cavity following spawning, females were categorized as completely spawned if they retained less than 0.5% of their eggs. Females that retained greater than 0.5% of their eggs were categorized as not completely spawned. In native populations, 50% of spawning females

are completely spawned before death (Hruska et al. 2011). To determine if females in the Sydenham River experienced greater egg retention than would be expected in their native range, a Pearson's chi-square goodness of fit test was used to compare observed egg retention from this population to that expected based on native Chinook salmon (e.g. 50% completely spawned). Egg retention values were arcsine transformed to normalize data represented as a percentage (Zar 1984).

A backwards stepwise multiple regression was done to determine the effect of temperature on egg retention. Temperature experienced by untagged females was estimated based on the average reproductive lifespan of tagged females (11 days) and river temperatures. The original model included reproductive lifespan, origin, and the interactions between temperature and origin, and between reproductive lifespan and origin. Non-significant interaction terms were sequentially dropped from the model followed by sequentially dropping non-significant factors. Linear regression was also used to determine the relationship between egg retention and the day of carcass recovery.

Results

Population sampling

Between 13 Sept - 13 Oct 2010, 63 females were tagged at the Owen Sound Mill Dam. Based on observations of settled females and the number of untagged females observed while observing tagged females, it was estimated that 25% of the females in this population that spawned upstream of the dam were tagged. Hatchery-reared fish represented 63.5% of all females tagged. There were no significant differences in fork length (two-sample t-test: $t_{df=58.33} = -0.22$, $p = 0.83$), weight (two-sample t-test: $t_{df=40.57} =$

-0.04, $p = 0.97$), percent fat (two-sample t-test: $t_{df=47.95} = -0.96$, $p = 0.34$), or fecundity (two-sample t-test: $t_{df=58.33} = -0.22$, $p = 0.83$) between hatchery-reared and wild females (Table 1). In addition there was no difference between the arrival schedules of hatchery-reared and wild fish (Kolmogorov-Smirnov: $D_{df=62} = 0.15$, $p = 0.88$; Figure 2).

Temperature

There was no difference among the eight temperature sensors (ANOVA: $F_{7,448} = 0.26$, $p = 0.98$) so all were used to calculate mean daily temperature. The mean daily water temperature of the spawning areas was related to the daily water temperature collected at the Environment Canada gauging station (regression: $F_{1,37} = 176.2$, $r^2 = 0.82$, $p < 0.001$; Figure 3a). The daily temperature collected at the Environment Canada gauging station was related to the daily discharge measured at the same location but the relationship was weak (regression: $F_{1,55} = 5.2$, $r^2 = 0.07$, $p = 0.03$; Figure 3b). Water discharge for the 2010 spawning season (Sep - Oct) appears to be on the high side compared to historical discharge (Figure 4). The number of tagged females on nests tended to increase as the spawning season progressed and as the river temperature decreased (Figure 5). Mean daily temperature during the spawning season was $12.9 \pm 2.8^\circ\text{C}$ and ranged between 7.4°C and 16.1°C (Figure 5). The number of females who were observed spawning at a higher temperature ($> 12.8^\circ\text{C}$) was higher than the expected number of zero, since it was hypothesized that no females would spawn above 12.8°C in their native range (Pearson's Chi-Square: $\chi^2 = 8.37$, $df = 1$, $p = 0.004$; Figure 6). Mean temperature

Table 1. Attributes [mean \pm s.e. (n)] of female Chinook salmon sampled between 13 Sept – 13 Oct 2011.

	Hatchery	Wild
arrival day	17 \pm 0.4 (40)	18 \pm 0.2 (23)
fork length (cm)	75.0 \pm 0.2 (40)	75.3 \pm 0.1 (23)
weight (kg)	5.2 \pm 0.0 (40)	5.2 \pm 0.1 (23)
fat (%)	0.9 \pm 0.0 (40)	0.9 \pm 0.0 (23)
fecundity	5490 \pm 20.4 (40)	5381 \pm 40.1 (23)
settled day	21 \pm 0.4 (21)	21 \pm 1.2 (8)
days on nest	6 \pm 0.4 (21)	6 \pm 0.2 (9)
reproductive lifespan (days)	11 \pm 0.2 (21)	11 \pm 0.2 (8)
egg retention (%)	35 \pm 6.8 (6)	12 \pm 3.5 (4)

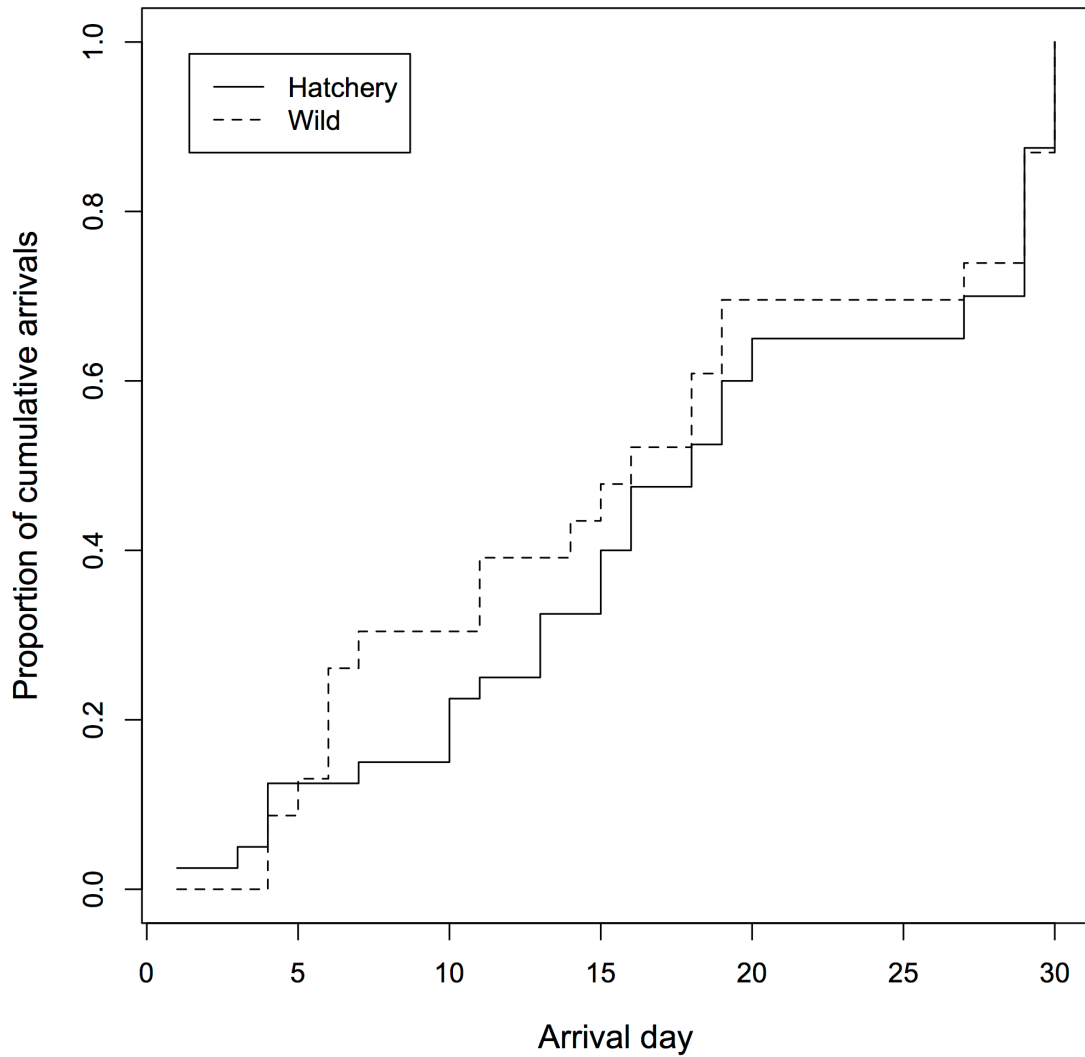


Figure 2. Cumulative proportion of arrivals for both hatchery (solid line) and wild (dotted line) female Chinook salmon tagged at the Owen Sound Mill Dam. An arrival day of one corresponds with the first date of tagging fish (13 September 2010). The cumulative proportion of arrivals did not differ between hatchery-reared and wild females.

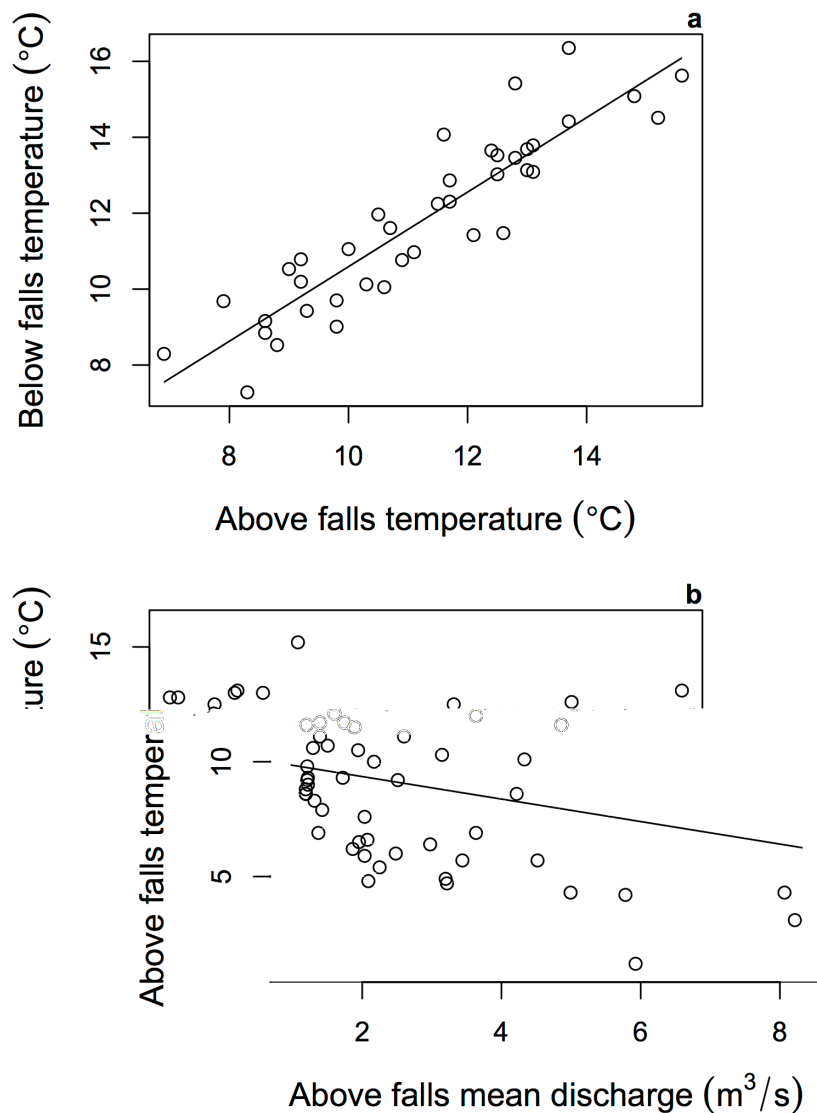


Figure 3. Panel (a) shows the relationship between the daily mean water temperature collected at Chinook salmon spawning locations in 2010 downstream from Inglis falls (below falls) and the daily mean water temperature collected from the Environment Canada gauging station (02FB007) located just upstream of Inglis Falls (above falls). Panel (b) shows the relationship between the daily mean water temperature and daily mean water discharge collected at the Environment Canada gauging station. Both lines indicate the results of the least-squares linear regression.

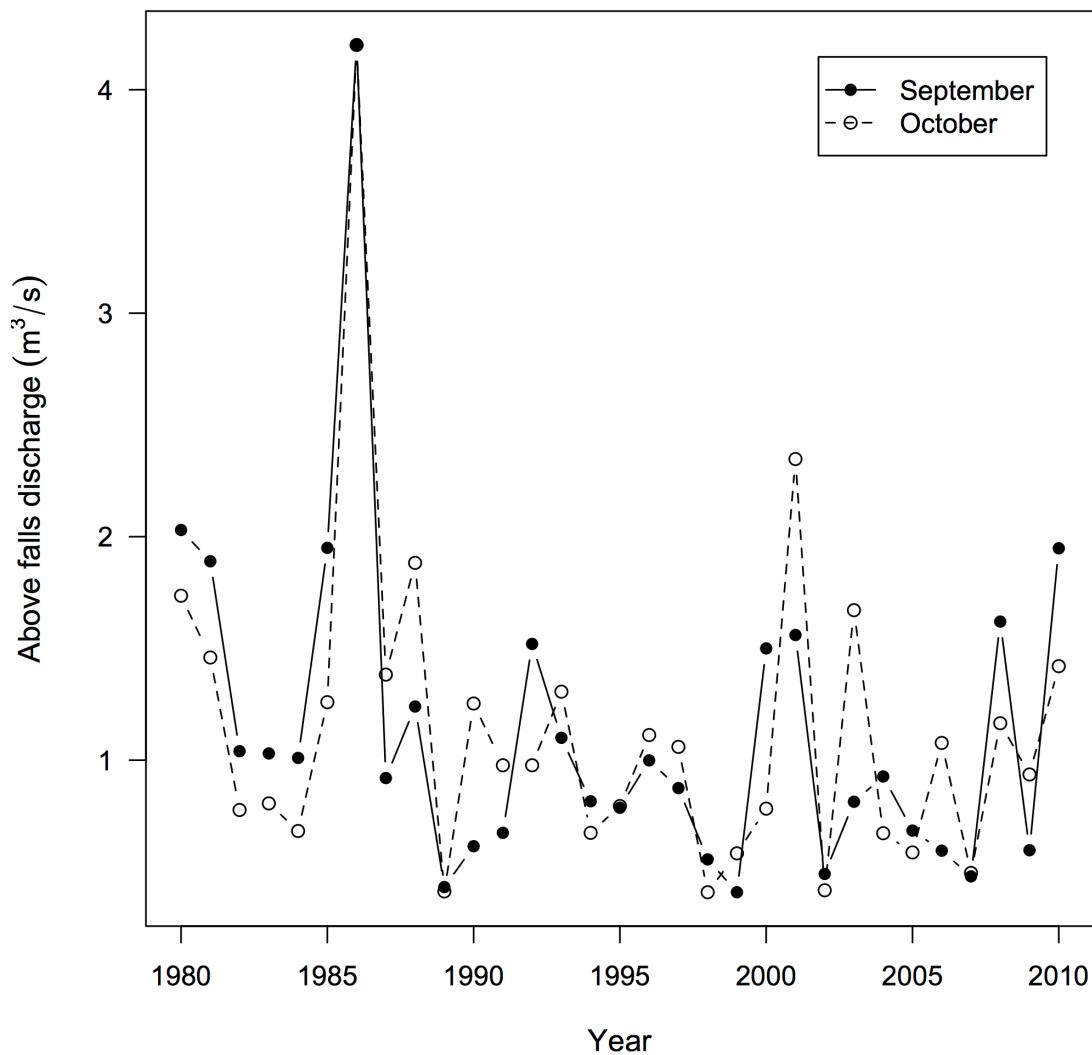


Figure 4. Mean discharge for the Sydenham River from 1980 – 2010 collected from the Environment Canada gauging station located above Inglis falls (02FB007). The solid dots connected by the solid lines show the mean discharge for the month of September. The open dots connected by the dotted lines show the mean discharge for the month of October.

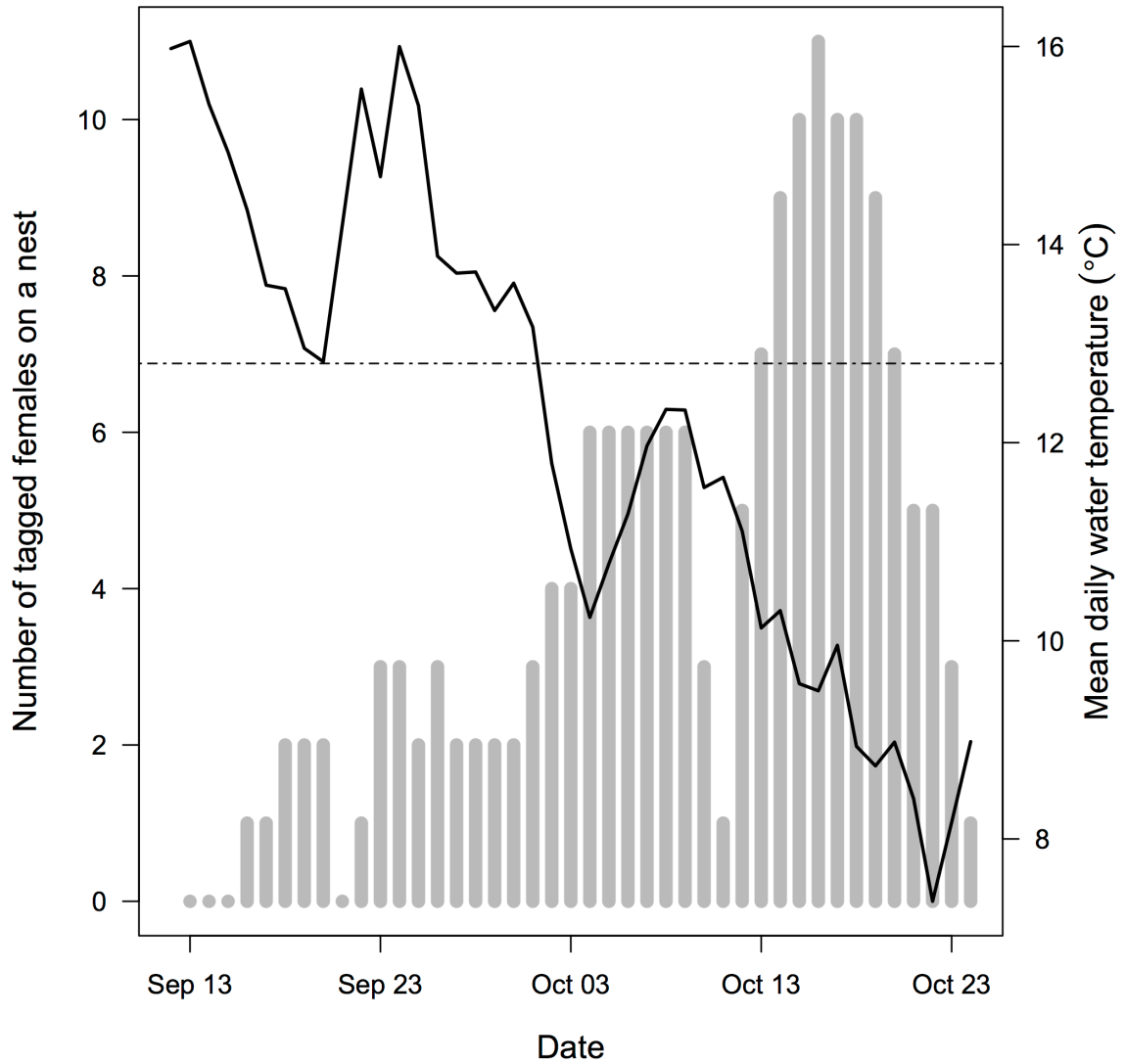


Figure 5. Grey bars show the number of tagged females on a nest for each observation date. The black line shows the mean river temperature on each date. The dotted line represents the upper limit (12.8°C) of temperatures typically experienced by spawning Chinook salmon in their native range.

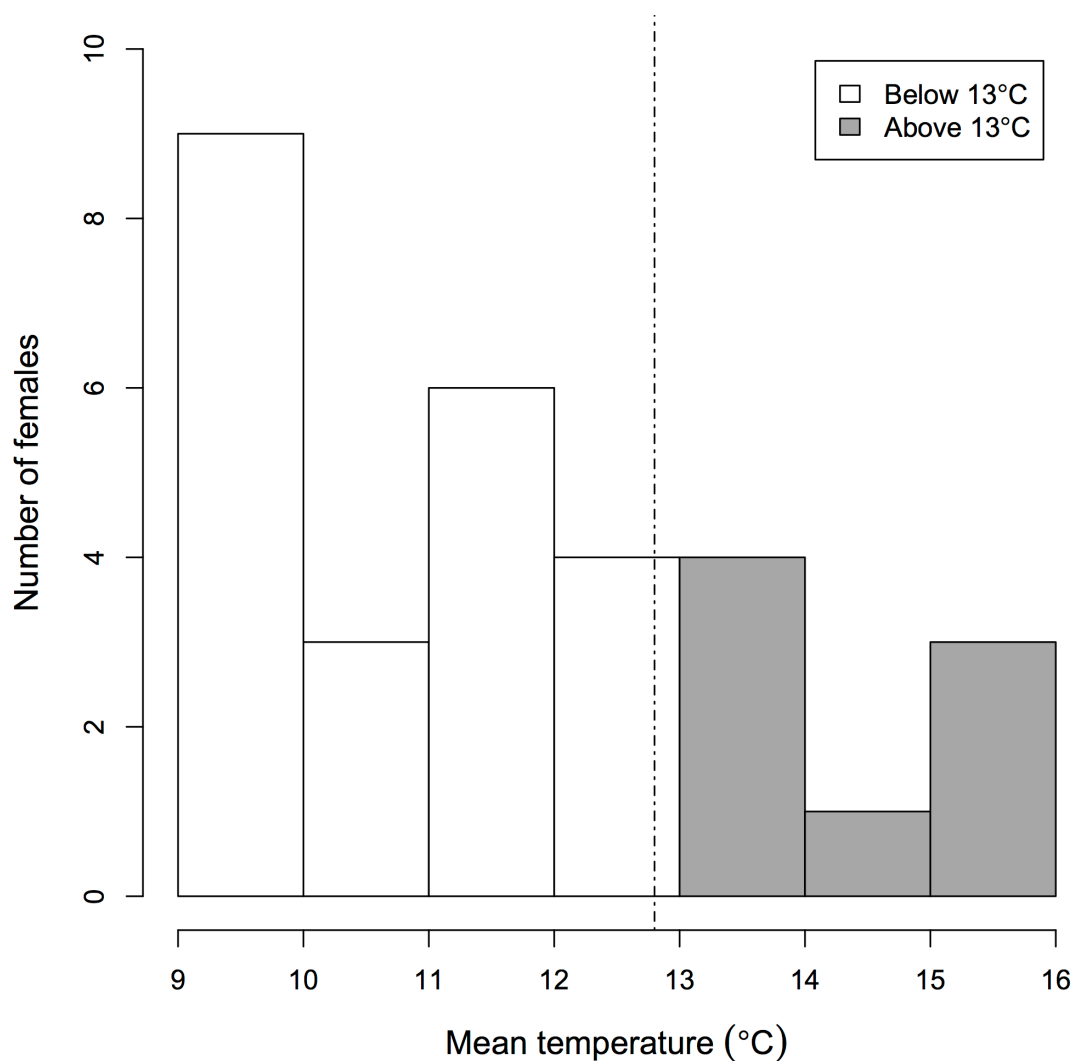


Figure 6. Frequency distribution of mean temperatures experienced by female Chinook salmon while nesting. Thirty percent of observed females nested at temperatures above the optimal level (shaded bars). Open bars show the females that nested at temperatures within the optimal level. The dotted line represents the upper limit (12.8°C) of temperatures typically experienced by spawning Chinook salmon in their native range.

experienced during spawning did not differ between hatchery-reared and wild fish (Student's t-test: $t_{df=18.83} = 0.15$, $p = 0.88$).

Reproductive lifespan

Contrary to prediction, there was no seasonal decline in reproductive lifespan (regression: $F_{1,28} = 0.57$, $r^2 = 0.02$, $p = 0.46$; Figure 7a) or percent fat at arrival (regression: $F_{1,27} = 0.008$, $r^2 = 0.0003$, $p = 0.93$; Figure 7b). Fish that had higher percent fat at arrival lived significantly longer than fish with less fat (regression: $F_{1,27} = 18.7$, $r^2 = 0.41$, $p < 0.001$; Figure 7c). There was no significant relationship between mean temperature experienced after tagging and reproductive lifespan (temperature effect in ANOVA: $F_{1,28} = 5.06$, $r^2 = 0.22$, $p = 0.06$; Figure 8) when effects of fork length on reproductive lifespan were accounted for.

Nest re-use

Directional selection resulting from nest re-use favored a later arrival day and settling day (Table 2). However, direct selection on nest re-use was not affected by reproductive lifespan or number of days on nest. Females that arrived earlier in the season were more likely to have their nests re-used (multiple logistic regression: $z_{df=27} = 2.5$, $p = 0.01$; Figure 9). There were no indirect effects of fork length ($z_{df=24} = -0.6$, $p = 0.56$), reproductive lifespan ($z_{df=24} = 0.6$, $p = 0.55$), or origin ($z_{df=24} = -0.3$, $p = 0.80$) on nest re-use.

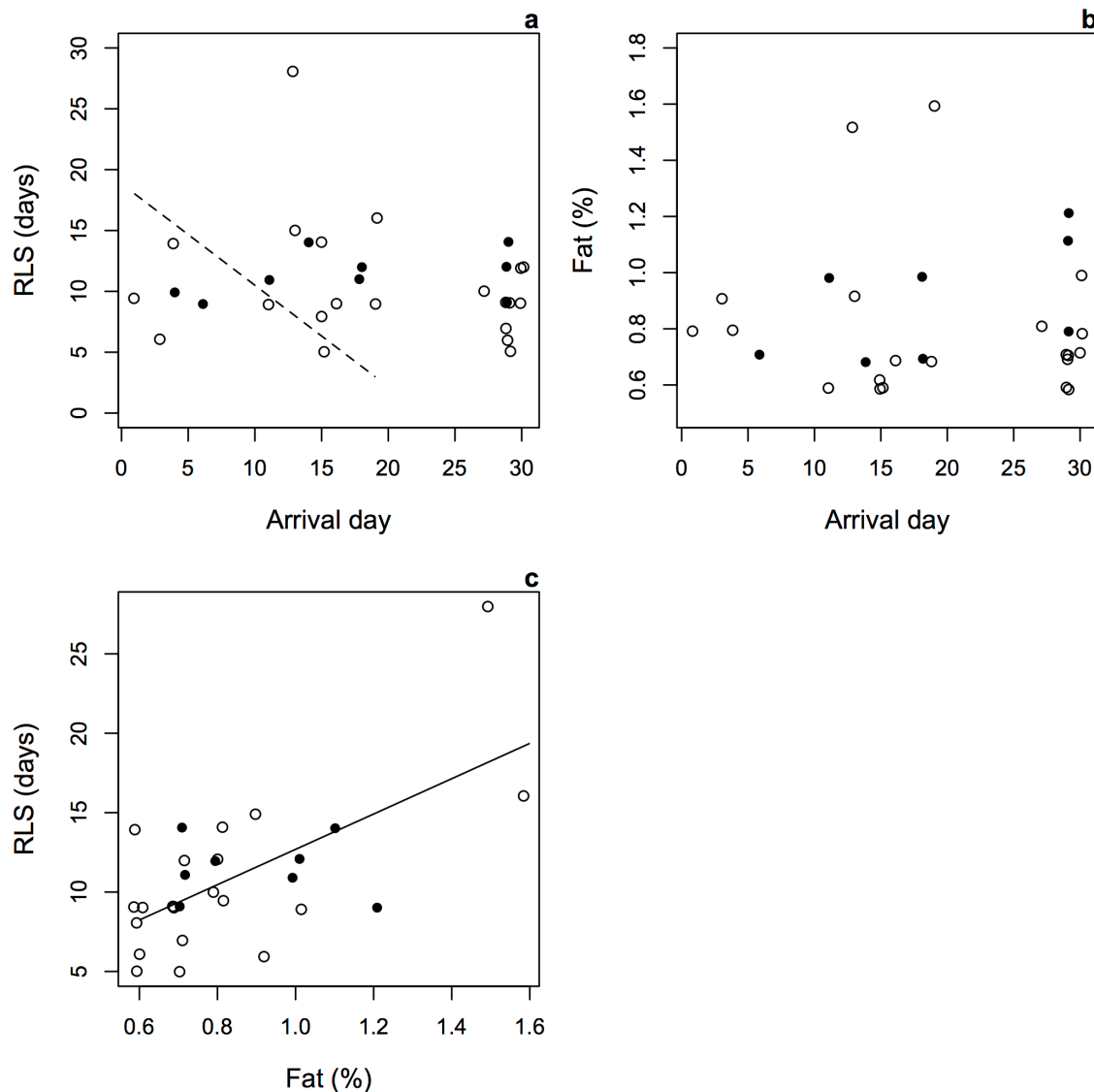


Figure 7. (a) Reproductive lifespan (RLS - number of days between tagging and death) as a function of arrival day (day tagged at dam) in wild (solid dots) and hatchery-reared (open dots) female Chinook salmon. No relationship was found between RLS and arrival day. The dotted line represents the seasonal decline of reproductive lifespan that typically occurs in native Chinook salmon populations (Hendry and Day 2005). (b) Percentage of fat at arrival as a function of arrival day in wild and hatchery-reared female Chinook salmon. No line represents that no relationship was found between percentage of fat at arrival and arrival day. (c) RLS as a function of percentage of fat at arrival in wild and hatchery-reared female Chinook salmon. The relationship between reproductive lifespan and percentage of fat at arrival indicates that individuals that had higher fat percentage at arrival lived longer.

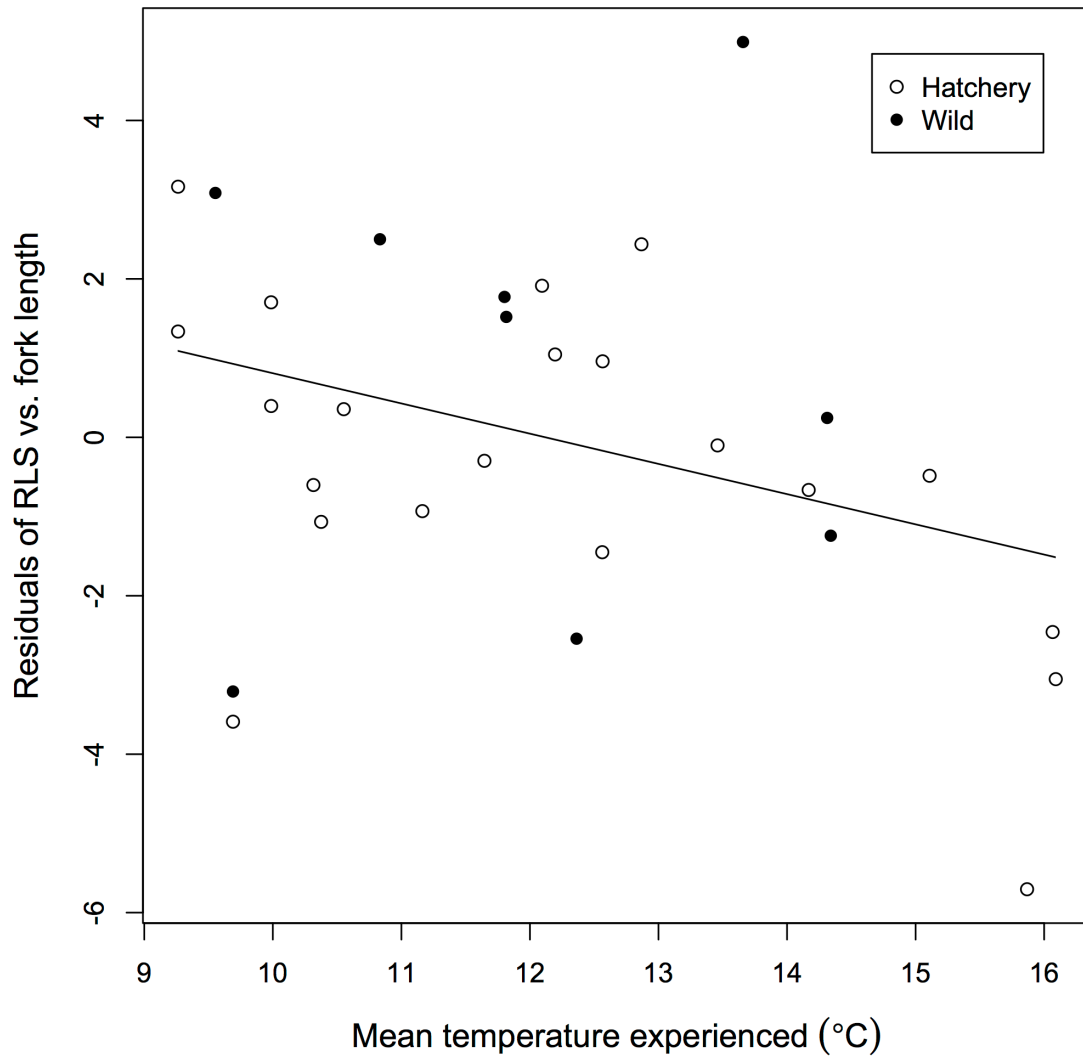


Figure 8. The residuals of reproductive lifespan (RLS) and fork length as a function of mean temperature experienced during RLS in wild (solid dots) and hatchery-reared (open dots) female Chinook salmon. The relationship between the residuals of the relationship between fork length and reproductive lifespan and average temperature experienced during reproductive lifespan (RLS) was not significant but it was in the expected negative direction.

Table 2. Estimates of how nest re-use imposes direct, directional selection on reproductive timing. Two models were run each including two traits. The coefficients from these regressions represent the strength of directional selection acting on each trait.

Trait	Logistic coefficient (\pm s.e.)	<i>p</i> -value
Model 1		
Arrival day	1.807 \pm 0.706	0.01
Reproductive lifespan	0.157 \pm 0.458	0.73
Model 2		
Breeding day	1.678 \pm 0.678	0.01
Days on nest	0.098 \pm 0.503	0.88

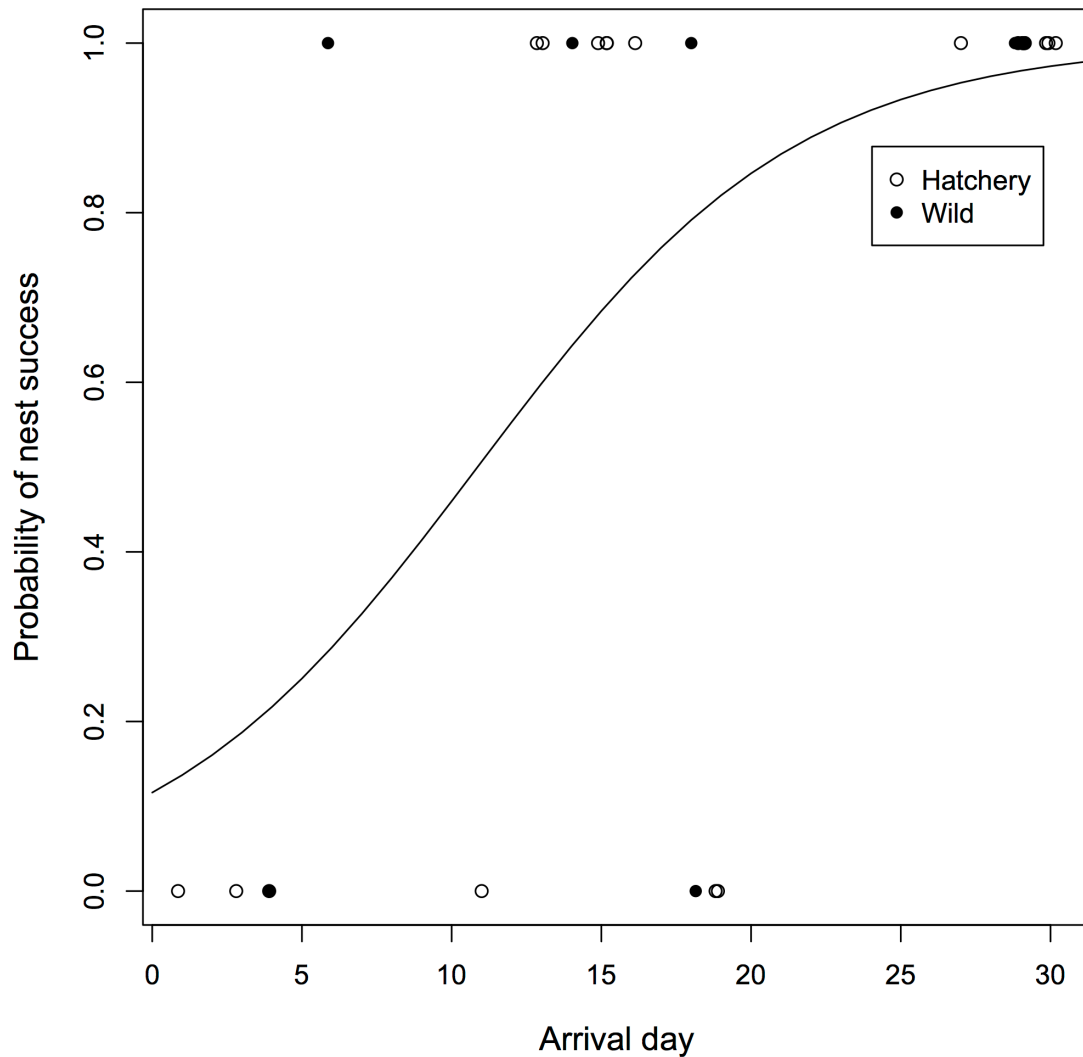


Figure 9. Logistic regression analysis of the relationship between the probability of nest success where 0 = re-used nests (*i.e.* unsuccessful), and 1 = not re-used nests (*i.e.* successful) and arrival day. Females that arrived earlier were more likely to have their nests re-used by later arriving females. An arrival day of one corresponds to the first date of tagging fish (13 September 2010).

Egg retention

Only one of the 20 females for which egg retention data were available (10 tagged, 10 untagged) was categorized as completely spawned. The observed percentage of females that completely spawned differed significantly from the expectation of 50% (Pearson's Chi-Square: $\chi^2 = 8.03$, $df = 1$, $p = 0.005$; Figure 10). However, the percentage of females that spawned completely did not differ between hatchery-reared and wild females ($\chi^2 = 0.03$, $df = 1$, $p = 0.86$). There was no correlation between egg retention and average temperature experienced after tagging (regression: $F_{1,18} = 1.86$, $r^2 = 0.09$, $p = 0.19$; Figure 11) although small sample size limits the strength of conclusions that can be drawn here. Similarly, there was no correlation between the day of carcass recovery and egg retention (regression: $F_{1,18} = 0.003$, $r^2 = 0.06$, $p = 0.96$; Figure 12).

Discussion

This study examined the effects of abiotic and biotic factors that influence reproductive timing, energy stores and egg retention in an introduced population of Chinook salmon. Since Chinook salmon have been reproducing in Lake Huron for less than 10 generations, local adaptation of these traits has most likely not occurred. Therefore, success of these rapid colonizers could be due to pre-adaptation. In the Sydenham River no seasonal decline in either reproductive lifespan or fat stores was found. Females had high egg retention and many females nested when water temperature was above optimal ($>12.8^\circ\text{C}$). These results indicate that fish are not pre-adapted to their novel environment. Instead, improper response to cues could be causing individuals to spawn in suboptimal conditions.

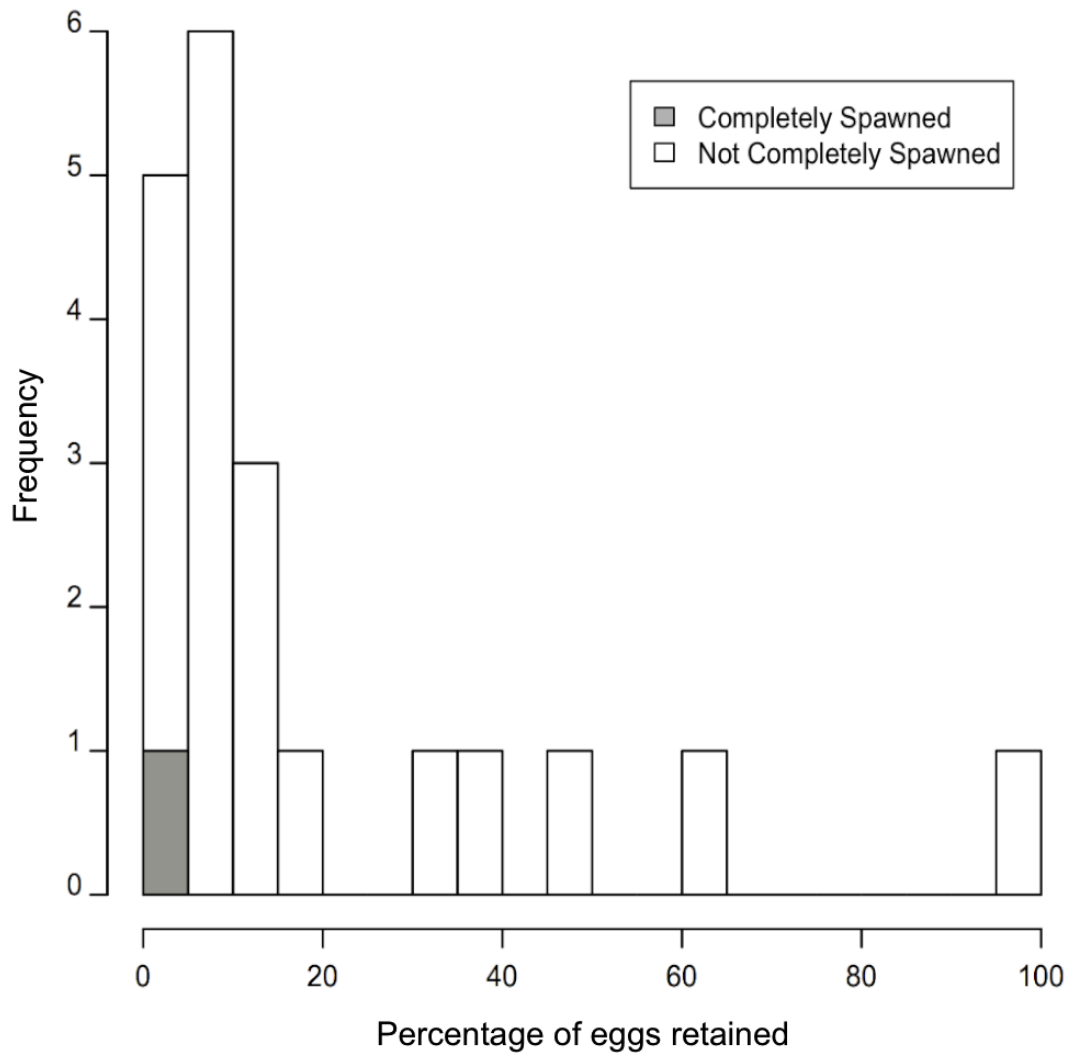


Figure 10. Frequency distribution of the percentage of eggs retained by female Chinook salmon ($n = 20$). The shaded area represents the one fish that was categorized as completely spawned ($< 0.05\%$ of eggs retained).

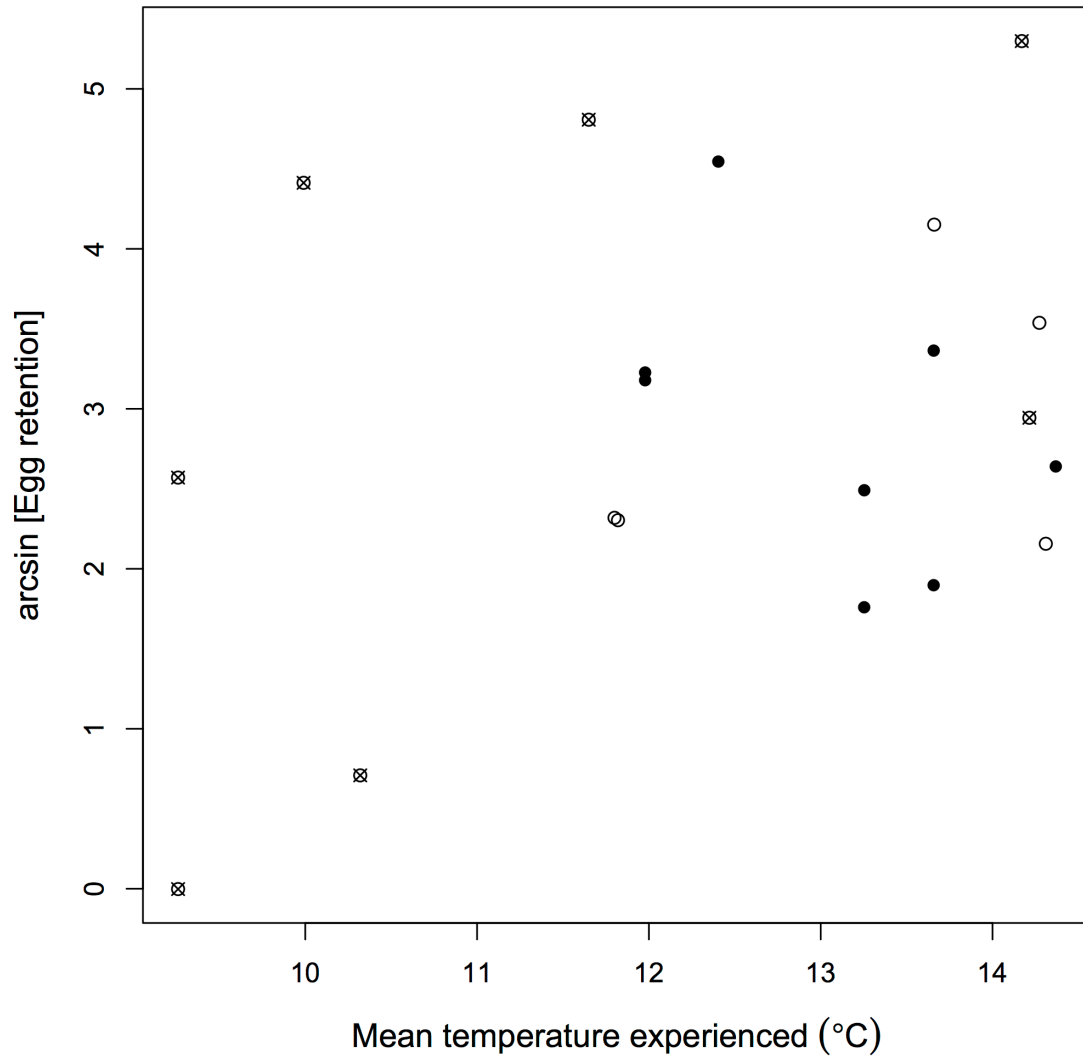


Figure 11. Egg retention as a function of mean temperature experienced during reproductive lifespan in female Chinook salmon of wild (solid dots), hatchery-reared (open dots with x) or unknown origin (open dots). Egg retention was not affected by temperature experienced since tagging or origin.

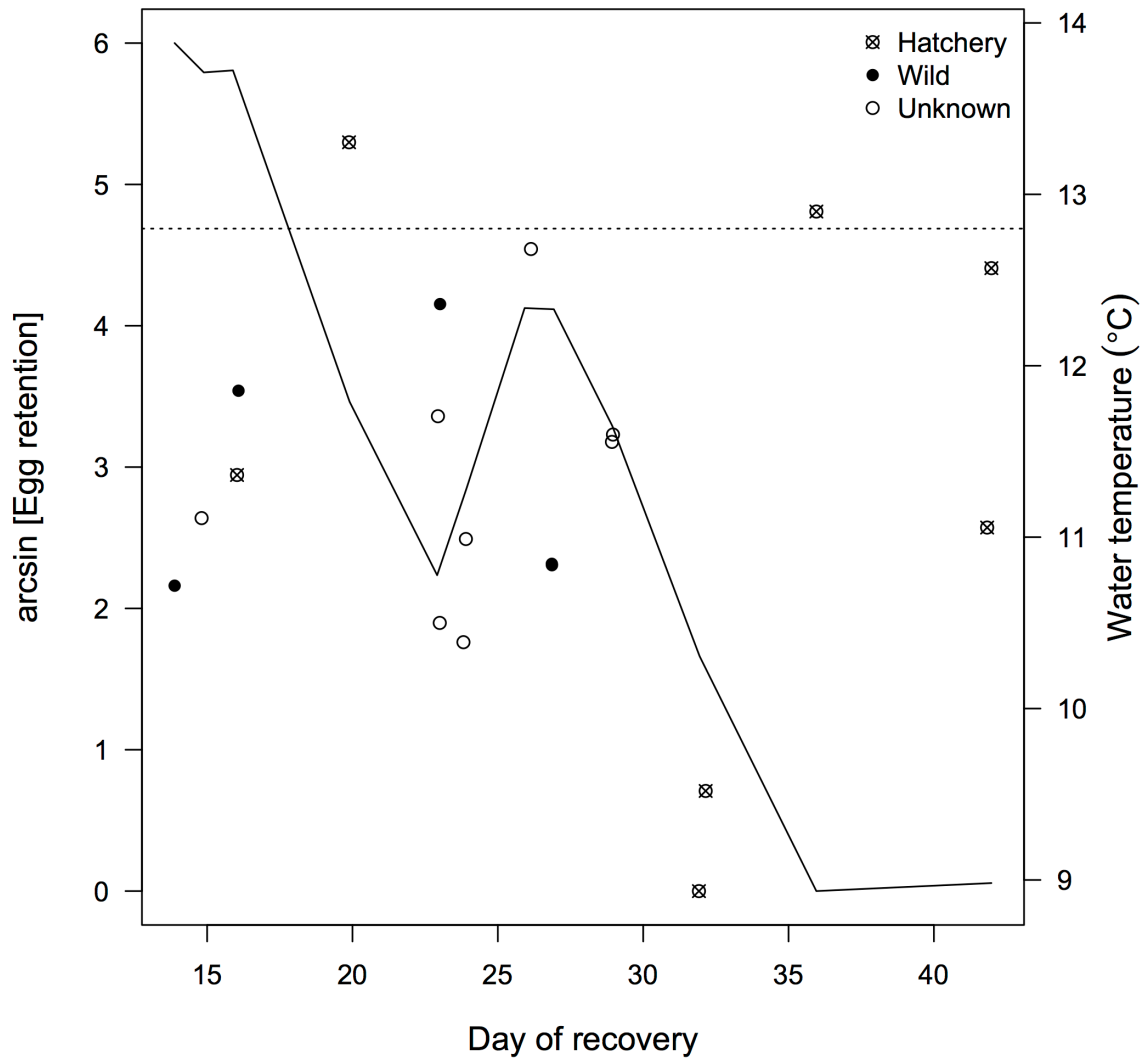


Figure 12. The relationship between egg retention and the day of carcass recovery in female Chinook salmon of wild, hatchery-reared, or unknown origin. The first carcass was recovered 13 days after the first female was tagged. The dotted horizontal line represents the upper limit of temperatures typically experienced by spawning Chinook salmon. The solid line shows water temperature ($^{\circ}\text{C}$) on each day of carcass recovery. There was no effect of origin on egg retention so it was dropped from the final model.

Population sampling

Hatchery-reared and wild Chinook salmon females did not differ significantly in fork-length, weight, percent fat, fecundity, or egg retention. There was also no difference in their arrival schedules, breeding day, the number of days spent on nests or reproductive lifespan. While differences between physical characteristics of hatchery-reared and wild fish were expected, both hatchery-reared and wild individuals interbreed in this population, which could prevent divergence between wild and hatchery-reared fish. The physical and life history similarities indicate that hatchery-reared and wild individuals have comparable adult characteristics regardless of the environmental differences experienced during incubation and the early stages of life after hatch. These similarities also indicate that data from hatchery-reared and wild individuals can confidently be pooled during subsequent analysis.

Temperature

The water temperature of the Sydenham River declined throughout the spawning season. Before the arrival of spawning fish, mean water temperature was 20°C (3 Sept) and water temperature decreased to as low as 7.2°C by the end of the season (22 Oct). The mean water temperature for the spawning period (13 Sept – 24 Oct) was approximately 12°C.

Mean daily water temperature measured above the falls was highly correlated with mean daily water temperature of the spawning areas below the falls. In addition, mean daily temperature of the spawning areas was negatively correlated with water discharge measured above the falls. The negative correlation between discharge and

water temperature indicates that high discharge events correspond to lower water temperature. The historical discharge that has been measured since 1980 reveals that in September 2010, Chinook salmon spawning in the Sydenham River experienced somewhat above average discharge than had been experienced in the previous 23 years. Since water temperature negatively correlates with water discharge this indicates that water temperature in 2010 may have been lower than temperatures previously experienced by spawning Chinook salmon in the Sydenham River.

The number of females on nests increased as river temperatures decreased over the fall. The mean temperature experienced by spawning females fell within the optimal temperature range for Chinook salmon although the number ($n = 9$) of individuals that spawned at temperatures above the optimal range was higher than what was expected ($n = 0$). Since Chinook salmon are a cold water species, individuals that experienced spawning temperatures higher than optimal could experience premature depletion of energy stores, increased susceptibility to disease (Wagner et al. 2005), and an increase in the percentage of eggs retained after spawning (Fukushima and Smoker 1997).

The mean daily water temperature did not differ among the eight sensors placed throughout the spawning locations, indicating that spawning sections of the river have little variation in water temperature. In using average temperature experienced over reproductive lifespan, I assumed that individuals did not use cold-water refuges.

According to Jonsson and Jonsson (2009), salmonids can exhibit behavioural thermoregulation and fish will seek out areas of cooler water during periods of waiting before spawning. In the 2010 spawning season I observed one cold-water flow into the spawning channel where many individual males would accumulate. I never witnessed

any females holding in this location which suggests that Chinook salmon of the Sydenham River exhibit similar spawning behaviours of their ancestral ocean-ecotype which typically spawn shortly after completing migration to spawning habitat (Healey 1991). Once a female has settled on a nest, where she will remain throughout spawning until death, she does not have the opportunity to seek colder refuges. Therefore using the total average temperature experienced since tagging should be a reliable estimate of the temperatures each female experienced while spawning.

In future studies, individual radio tags with temperature sensors could be used to give very accurate measurements of temperature experienced throughout the spawning period. However, not only are these transmitters costly, the use of similar transmitters has recently been found to negatively affect reproductive lifespan (Warren and Morbey, unpublished data). Since accurately determining reproductive lifespan was a fundamental part of this study, the effects of radio transmitters on reproductive lifespan should be examined further to determine if they would be appropriate to use in future studies.

Reproductive lifespan and nest site re-use

Contrary to my original prediction, no seasonal decline in reproductive lifespan was found. The average number of days for a female to defend a nest in the Sydenham River was only six days after breeding occurred. By contrast, Chinook salmon in their native range (Nechako River, B.C.), have been found to defend nests from 6 – 25 days, with early arriving fish having longer defense times (Neilson and Banford 1983). This seasonal decline in reproductive lifespan is a typical trade off that can be found in most

salmon populations (Morbey and Ydenberg 2003; Hendry and Day 2005). Fish that arrive early have access to prime habitat but must contain greater fat stores to fuel the defense of their nest from later arriving females since nest re-use is common upon the death of defending females. Females that arrive late in the season may have less of a choice in habitat, but do not need to live as long to defend their nest from even later arriving females. This trade off is typical and indicates that fish that arrive later could benefit from allocating energy to reproductive investment instead of body fat stores to fuel nest defense (Hendry et al. 2004).

No decline in fat stores with arrival day was found. However, fish that had a higher percentage of fat at arrival lived longer than fish with less fat, after controlling for arrival day. This suggests that the fat meter appropriately measured relative energy upon arrival to the spawning grounds. This also suggests that in the Sydenham River system, individuals may have little stored fat upon arrival to spawning grounds, compared to populations in the Pacific Northwest, and are thus unable to sustain long periods of nest defense. It is also possible that individuals may have experienced conditions at some point during migration that depleted energy stores. For example, in a multi-year study of kokanee salmon, longer reproductive lifespans were found in the coolest year of the study (Morbey and Ydenberg 2003). Therefore in the Sydenham River, higher temperatures at the beginning of the season could be depleting these small finite amounts of energy at a faster rate than the later arriving females that experience cooler temperatures.

Shorter reproductive lifespans than typical of Chinook salmon combined with potentially lower percentage of fat upon arrival could imply that there are limiting resources available for growth in Lake Huron. Since Chinook salmon were introduced to

Lake Huron in the 1960s there has been a steady decline in the number of prey fish available due to large numbers of large predatory fish (Paterson et al. 2009). Although there are no studies that indicate a decline in percentage of fat of individuals throughout this period, the decline in prey fish has coincided with an increase in older fish at spawning. This pattern suggests that fewer resources have led to a delay in maturation of adult fish (Dobiesz et al. 2005). In addition, local sport fishermen of the SSA have commented anecdotally on the decreased size of adult Chinook salmon in recent years.

Females that arrived to spawn earlier in the season likely have less successful nests because of nest site re-use by later arriving females. Significant directional selection on arrival day and breeding day imposed by nest site re-use was found, indicating that at this life-history stage, selection is acting on females to arrive later in the season. However, no significant directional selection was found on reproductive lifespan.

Temperature and reproductive lifespan

There was no significant effect of mean temperature experienced on reproductive lifespan. However, the observed relationship was in the expected negative direction. Interestingly, since the historical discharge data suggests that water temperature for the 2010 spawning season was most likely cooler than previous years, the effect of temperature on reproductive lifespan may be more apparent in years where water temperature is higher. It is difficult to compare the effect of temperature within a natural environment because all early arriving fish should have the same level of reproductive investment as would all of the later fish, because of the trade-off between arrival day and

energy allocation for reproduction. Manipulating the temperature of the river in order to have both early arriving and late arriving fish exposed to the same temperatures would give more direct insight to how temperature affects reproductive lifespan. However, in a natural spawning setting this would be impractical and logistically very difficult.

Egg retention

Egg retention was higher than typically expected of salmon in their native range. Only one of twenty individuals had completely spawned in the Sydenham River. Since Chinook salmon females will spawn their eggs in a series of spawning events over a few days, higher egg retention could be another consequence of females in the Sydenham River not living long enough to complete the necessary spawning events to void all of their eggs. In their native range, female Chinook salmon have been found to have higher egg retention when they experience frequent harassment while spawning (Healey 1991). The spawning locations in the Sydenham River are located near public parks and people and dogs were frequently seen physically disturbing settled Chinook salmon females, which could explain why egg retention was higher in this population. Temperature could also affect the percentage of eggs retained, through effects on reproductive lifespan, for example females not living long enough to spawn all of their eggs.

Temperature and egg retention

While higher egg retention has been found when individuals experience warmer water temperatures (Fukushima and Smoker 1997), in this study there was no effect of temperature experienced after tagging on the number of eggs retained. However, the low

sample size constrains the ability to make a strong conclusion about the effect of temperature on egg retention. This may indicate that another factor such as human disturbance might be responsible for the higher than expected number of fish that did not spawn completely. While it was hypothesized that carcasses recovered for egg retention later in the season might have lower egg retention, because presumably those fish would have spawned at lower temperatures, there was no relationship between day of carcass recovery and egg retention. Temperature could also indirectly affect the percentage of eggs retained if higher temperatures reduced reproductive lifespan and individuals did not live long enough to spawn all of their eggs.

Cues and spawning conditions

Based on the results of this study, Chinook salmon females in the Sydenham River do not appear pre-adapted to spawn at the locally appropriate time. Trade-offs and reproductive success typical of Chinook salmon in their native range were not found. There was no seasonal decline in reproductive lifespan nor a corresponding decline in fat stores, egg retention was higher than that typical of native populations, and many females spawned at temperatures higher than that preferred in their native range. This could indicate that the cues that trigger Sydenham River Chinook salmon to migrate upstream cause females to experience suboptimal conditions on the spawning grounds.

A change in photoperiod typically triggers initial migration of Pacific salmonids to freshwater (Clarke et al. 1994; Quinn and Adams 1996) and other environmental cues, such as water temperature and flow, initiate freshwater entry and subsequent migration to spawning habitat (Jonsson and Jonsson 2009). The cues that Lake Huron Chinook

salmon inherited from their Green River ancestors may trigger individuals to begin migration at the appropriate time for the Green River population but not for the Sydenham River.

In a comparison of arrival day and day length between the Green River population and the Sydenham River population both mean arrival day and day length are similar between the two sites (Quinn et al. 2002; Table 3). This suggests that Sydenham River Chinook salmon could be responding to photoperiod to initiate migration. Intriguingly, when the average temperatures of each location are considered on that shared arrival day, the temperature of the Sydenham River is a few degrees warmer than that of the Green River. While this difference is about 3°C, it is important to note that the temperature in the Sydenham for the arrival date of 1 Oct is only for 2010. The discharge data suggests that the water temperature for 2010 may be cooler than the temperatures experienced in previous years. In addition, the average annual surface temperature of the Green River is only 9.8°C and temperatures do not exceed 15°C at any point during the year (Quinn et al. 2002). Even in 2010, mean Sydenham River temperatures reached 20°C in the months preceding spawning. If individuals in the Sydenham River are responding to the proper cues of photoperiod that are similar to their native habitat of the Green River but arriving when temperatures are too warm this would negatively affect the reproductive success of early arrivals.

Founder effects from individuals that strayed to spawn in the Sydenham River could also account for mistiming of reproduction in this population. Founder effects are common in populations of introduced salmonids either because a small number of

Table 3. Mean arrival date, day length on arrival date, and mean temperature at arrival for the Green River, WA, USA (ancestral population) and the Sydenham River, ON (current study).

	Green River	Sydenham River
Location	Auburn, WA	Owen Sound, ON
Latitude, Longitude	47°18'N, 122°12'W	44°34'N, 80°56'W
Mean arrival date	30 September	1 October
Day length on arrival date	11 hrs. 41 min.	11hrs. 43 min.
Temperature on arrival date	~10°C	13.2°C

individuals are chosen by hatchery groups from the large native population for introduction or because only a few strays may initially colonize a new site (Salmenkova 2008). The individuals that were first stocked into the Michigan side of Lake Huron in the early 1960s only represented a small portion of the genetic variation of the Green River population. Following the Chinook salmon introduction, evidence of Chinook salmon spawning in Lake Huron tributaries was first found in the Sydenham River in the early 1980s. Adults that strayed to spawn in the Sydenham River were assumed to be from stocked adults from the Michigan side of Lake Huron since stocking in Ontario waters did not begin until the mid 1980s (Crawford 2001; Weeder et al. 2005). The founders that strayed to the Sydenham River were probably a small subset of the introduced Lake Huron population. Studies have suggested that initial non-representative founders like these could be favoured in populations of rapidly colonizing introduced salmonids (Quinn et al. 2001). For example, traits such as high energy reserves might cause initial founders of a newly colonized river with a long migration distance to be more successful in that new environment (Quinn et al. 2001). However, in the Sydenham River, if the initial founders were disproportionately early spawners it would cause future generations to migrate early as well. If suboptimal environmental conditions are experienced after early arrival that correspond with a decrease in reproductive success, selection should favour later arrivals that correspond with optimal spawning conditions and increase reproductive success. Even though salmon are known to rapidly adapt in suitable environments since reproductive timing is highly heritable (Smoker et al. 1998; Stewart et al. 2002), adaptation of the Sydenham River population of Chinook salmon

may be slowed because of ongoing hatchery supplementation, which favours early arrival.

There was no effect of origin (hatchery-reared or wild) on the reproductive patterns examined. However, influences of hatchery-reared fish are common and the hatchery practices of the local sport fishing clubs may be inadvertently selecting for early-arriving fish. The Sydenham River is where the majority of the eggs are collected to maintain hatchery practices and stocking efforts of Lake Huron. The local sportsmen's associations that are permitted to take eggs prefer to have their eggs as early in the spawning season as possible. As a result, groups begin collecting gametes as soon as consistent numbers of reproductively mature females begin arriving at the Mill Dam. The sportsmen's associations keep collecting eggs until they reach their maximum quota that is allowed by the Ontario Ministry of Natural Resources. In the 2010 spawning season, the egg take lasted only six days, beginning on 3 Oct 2010. Assuming a high heritability of spawning timing (Smoker et al. 1998), rearing gametes only from individuals that arrive earlier in the season would cause more individuals to inherit the trait to arrive earlier to spawn. Individuals in the wild that arrived too early when temperatures are too warm might have lower reproductive success and if they were unsuccessful, would not pass on the trait to arrive early to future generations. While higher than optimal temperatures experienced during earlier spawning should be selecting for the later arrival of individuals, early gamete collection by hatchery groups opposes this selection and ensures that early arrivals are favoured. There was no significant difference in the arrival schedules of hatchery-reared and wild individuals in 2010; however, Chinook salmon in Lake Huron have only been reproducing for 10 generations

since their introduction (Suk et al. 2011) and hatchery and wild component are mixed. If collection of gametes continues in this manner it could cause a significant shift in breeding date in the future or will continue to contribute to poor reproductive success.

Similar results were shown in a long-term study of the ancestral population that examined the breeding date of Chinook salmon in the Green River, Washington USA. Results of that study showed that selection imposed by hatchery practices led to a significant shift to spawn earlier even though water temperature increases should have selected for later spawning (Quinn et al. 2002). Further studies should compare reproductive timing of the Chinook salmon in the Sydenham River to other tributaries such as the Nottawasaga River, a tributary that maintains a large successful naturally reproducing population with no hatchery influences. Further study would reveal whether or not the hatchery practices in the Sydenham River are negatively affecting the timing of individual Chinook salmon in Lake Huron.

Conclusion

While it is known that Chinook salmon populations in Lake Huron can reproduce in the wild, the population spawning in the Sydenham River does not appear to be spawning under optimal conditions. No seasonal decline in reproductive lifespan or a corresponding decline in fat stores, higher egg retention and individuals spawning above optimal temperatures indicate that this population is arriving too early to spawn successfully. A mismatch in cues that initiate spawning may contribute to the mis-timing of this population. However, it is likely that hatchery gamete collection also has an effect

on the reproductive timing of this population. Specifically, inadvertent artificial selection favouring early arrival is opposing natural selection favouring late arrival.

While the Sydenham River Chinook salmon population appears to be performing sub-optimally at the reproductive stage, other studies have suggested that the majority of the Chinook salmon in Lake Huron are the result of natural reproduction. This could be due to higher reproductive output from other Lake Huron tributaries or due to greater success at other life history stages (e.g. adult foraging). Continued investigation on the reproductive timing of the Sydenham River Chinook salmon population could give further insight into how the combination of environmental factors and hatchery practices (e.g. natural and artificial selection) influence the rate of adaptation of reproductive timing in newly established populations.

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Appendix 1. UWO approved animal care protocol (2010-2011)



05.01.2010

***This is the 2nd Renewal of this protocol**

*A Full Protocol submission will be required in **04.30.2012**

Dear Dr. **Morbey**

Your Animal Use Protocol form entitled:

The evolutionary ecology of reproductive timing and senescence in Pacific salmon

has had its yearly renewal approved by the Animal Use Subcommittee.

This approval is valid from **05.01.2010 to 05.01.2011**

The protocol number for this project remains as **2008-077**

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.

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.

The holder of this *Animal Use Protocol* is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.

c.c. S. Waring, W. Lagerwerf

The University of Western Ontario
Animal Use Subcommittee / University Council on Animal Care
Health Sciences Centre, ● London, Ontario ● CANADA – N6A 5C1
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Professional Experience

Recovery Planning Biologist **Jan – Mar 2012**
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Species at Risk Biologist **Jun, Jul; Oct-Dec 2009**
 Environment Canada – Canadian Wildlife Service, Ontario
Field Technician **Aug – Oct 2009**
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Park Steward **May 2003 – Apr 2005**
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 Maple Leaf Award for service to college community (SUNY-ESF) **2002**
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Conference Presentations

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