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# Maternal Effects and the Evolution of Chinook Salmon

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# Abstract

Pacific salmon (*Oncorhynchus* spp.) populations are under increasing threat due to habitat degradation, over fishing, invasive pathogens, and climate change. The early life history stage (fertilization – free feeding) is one of the most vulnerable developmental phases and performance at this stage may be a critical factor affecting population persistence. Offspring traits and performance are often greatly influenced by maternal effects, which have the potential to alter patterns of inheritance and selection, and environmental factors such as temperature. However, the contribution of maternal effects to the evolution of offspring traits under varying environmental conditions is still poorly understood in salmon. To address this research gap, I assessed the contribution of egg size, a primary maternal effect trait, to the within and among population variation in offspring traits in Chinook salmon (*Oncorhynchus tshawytscha*) under different rearing temperatures. I found that egg size explained most of the within and among population variation in offspring traits, which suggests that egg size has the capacity to significantly influence the adaptive response of early life phenotypes. I also assessed the effect of egg nutrient composition, which is a transgenerational maternal effect, on the expression of offspring phenotypes and determined that both the fatty acid and proximate composition of eggs influenced offspring phenotypes above and beyond the effect of egg size. Importantly, the effects of both egg size and nutrient composition were temperature dependent. A primary concern for many studies of maternal effects is the lack of in-situ studies. Therefore, I reared Chinook salmon embryos in-situ and found that egg size had a linear, non-linear, or no effect on early life survival depending on the habitat characteristics of the nest. Based on the in-situ egg size – survival relationships, I showed how variation in egg size could increase or decrease offspring production in a population depending on the match between the population egg size distribution and the egg size selection regime using a simulation model. Overall, this work demonstrates the significant contribution maternal effects make to the expression and evolution of offspring phenotypes in salmon.

## Keywords

Maternal Effect, Heritability, Quantitative Genetics, Egg Size, Egg Nutrients, Fatty Acid, Transgenerational Effect, Environment, Redd, Offspring, Chinook Salmon

# Co-Authorship Statement

Two of the data chapters in this dissertation have been published in peer-reviewed publications, and a third is ready for submission. The abstracts of the published manuscripts have been incorporated into the introduction of this dissertation, while the main body of the manuscripts are contained in the data chapters. The supplementary materials of the published manuscripts can be found in the appendices. The formatting of the manuscripts was changed to reflect that of the entire dissertation (e.g., font type and size, point of view).

A version of Chapter 2 is published in the journal Evolutionary Applications [Thorn, M.T., Morbey, Y.E. (2018). Egg size and the adaptive capacity of early life history traits in Chinook salmon (*Oncorhynchus tshawytscha*). Evolutionary Applications 11(2): 205-219. doi: 10.1111/eva.12531]. MT designed the study, collected and analyzed the data, wrote the manuscript, and is the corresponding author. YEM provided advice on the study design and data analysis, provided funding, and edited the manuscript.

A version of Chapter 3 is published in the Canadian Journal of Fisheries and Aquatic Sciences [Thorn, M.T., Dick, M.F., Oviedo, L., Guglielmo, C.G., and Morbey, Y.E. (2018). Transgenerational effects of egg nutrients on the early development of Chinook salmon (*Oncorhynchus tshawytscha*) across a thermal gradient. Canadian Journal of Fisheries and Aquatic Sciences. In Press. doi: 10.1139/cjfas-2018-0013]. MT designed the study, collected and analyzed the data, wrote the manuscript, and is the corresponding author. MFD assisted with the fatty acid analysis and edited the manuscript. LO assisted with hatchery rearing and fatty acid analysis. CGG provided the laboratory equipment for the fatty acid and proximate composition analysis, and edited the manuscript. YEM provided advice on the study design and data analysis, provided funding and hatchery facilities, and edited the manuscript.

Chapter 4 will be submitted for publication to Transactions of the North American Fisheries Society [Thorn, M.T., Morbey, Y.E. (2018). Survival under the gravel: the effect of egg size and parental identity on the in-situ hatching success of Chinook salmon

(*Oncorhynchus tshawytscha*)]. MT designed the study, collected and analyzed the data, wrote the manuscript, and is the corresponding author. YEM provided advice on the study design and data analysis, provided funding, and edited the manuscript.

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# List of Abbreviations and Symbols

| | |
|---|---|
| ANCOVA | Analysis or Covariance |
| ANOVA | Analysis of Variance |
| ARA | Arachidonic Acid (20:4n-6) |
| CI | Confidence Interval |
| CR | Credit River |
| DHA | Docosahexaenoic Acid (22:6n-3) |
| DO | Dissolved Oxygen |
| EPA | Eicosapentaenoic Acid (20:5n-3) |
| FA | Fatty Acid |
| MUFA | Monounsaturated Fatty Acid |
| PC | Principal Component |
| PCA | Principal Component Analysis |
| PERMANOVA | Permutational Multivariate Analysis of Variance |
| PR | Pine River |
| PUFA | Polyunsaturated Fatty Acid |
| SD | Standard Deviation |
| SE | Standard Error |
| SFA | Saturated Fatty Acid |
| SR | Sydenham River |
| TME | Transgenerational Maternal Effect |

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# 1 General Introduction

Ecology and evolution have traditionally been treated as minimally interacting disciplines because ecology occurs on short time scales (days-years) and evolution occurs on long time scales (hundreds-millions of years). Recently, researchers have realized that evolution can occur on ecological timescales (Hendry & Kinnison, 1999; Kinnison & Hendry, 2001; Reznick & Ghalambor, 2001) and that evolution can interact with ecological processes in what is known as eco-evolutionary dynamics (Fussmann, Loreau, & Abrams, 2007; Hairston, Ellner, Geber, Yoshida, & Fox, 2005; Hendry, 2016; Thompson, 1998). The phenotype of an organism can change between generations and such a shift in phenotype can influence how an organism interacts with the environment by altering rates of consumption and storage as well as patterns of habitat use (Bassar et al., 2010; Post & Palkovacs, 2009). Ultimately, these evolutionary shifts in individual phenotype can scale up to changes in population growth/size between generations and affect overall ecosystem functioning (Hairston et al., 2005; Kinnison & Hairston, 2007; Yoshida, Jones, Ellner, Fussmann, & Hairston, 2003). Furthermore, feedbacks can occur between ecological and evolutionary processes (Post & Palkovacs, 2009). Predicting these eco-evolutionary dynamics will require an in-depth understanding of the contemporary evolution of phenotypes (i.e., evolution that occurs on ecological time scales) in response to environmental variation.

Phenotypes are the way in which individuals interact with their surrounding environment and an individual's phenotype is broadly determined by genetic, maternal, and environmental sources of variation (Lynch & Walsh, 1998). Studies of contemporary evolution have generally focused on quantifying the per-generation degree of phenotypic change attributable to direct genetic effects (Reznick & Ghalambor, 2001). Though there is sound reasoning behind this focus, namely to confirm a genetic basis of phenotypic change, researchers have often neglected the maternal component of phenotypic variation because it is often thought of as a nuisance source of environmental variation (Falconer & Mackay, 1996; c.f. Wade, 1998). Yet, the maternal component of variation is more than an environmental effect and is particularly important to the expression of early life

phenotypes (Bernardo, 1996; McAdam, Garant, & Wilson, 2014; Mousseau & Fox, 1998a; Räsänen & Kruuk, 2007; Wilson & Réale, 2006). Because early life survival is low for many species, selection acting on early life phenotypes can have a strong influence on the distribution of adult phenotypes (Goodrich & Roach, 2013; Metcalfe & Monaghan, 2001) and on population vital rates (i.e., population growth; Benton, Plaistow, Beckerman, Lapsley, & Littlejohns, 2005; Venturelli et al., 2010). Therefore, we need to understand how the maternal components of phenotypic variation influence early life traits before we can fully understand contemporary evolution.

## 1.1 Maternal Effects and Evolution

Maternal effects occur when the phenotype of a mother influences the phenotype of her offspring beyond the direct effect of genes underlying the offspring trait (Marshall & Uller, 2007; Mousseau & Fox, 1998b; Räsänen & Kruuk, 2007). Maternal effects are mediated by maternal traits (i.e., maternal effect traits) and fall into two broad categories: 1) pre-zygotic maternal effects; and 2) post-zygotic maternal effects (Mousseau & Fox, 1998a). Pre-zygotic maternal effects are those that occur prior to gamete fertilization and cannot be altered post-fertilization, such as egg nutrient content, egg size/number, or mate choice (Mousseau & Fox, 1998a). Post-zygotic maternal effects are those that occur after gamete fertilization, such as lactation or nest guarding (Mousseau & Fox, 1998a). Depending on the organism, both pre- and post-zygotic maternal effects constitute the maternal component of variation for an offspring phenotype.

Traditionally, the response of a trait to selection has been predicted in the absence of maternal effects using the breeder's equation, whereby a change in phenotype between generations ($\Delta z$) is predicted by multiplying the additive genetic variation of the trait ($V_A$) and the directional selection gradient ($\beta$) acting on the trait ($\Delta z = V_A \cdot \beta$; Falconer & Mackay, 1996). However, this simple model of trait evolution has rarely provided accurate predictions regarding the response of a trait to selection (Merilä, Sheldon, & Kruuk, 2001). Part of the inaccuracies of the breeder's equation stems from its exclusion of maternal effects. When maternal effects are included, the response of a trait to selection ($\Delta z$) becomes much more complex and can be predicted using the following equation:

$$\Delta z = \left(G_{oo} + \frac{m}{2} G_{mo}\right)\beta_{o,t} + G_{mo}\beta_{m,t} + m\left(G_{mo} + \frac{m}{2} G_{mm}\right)\beta_{o,t-1} + mG_{mm}\beta_{m,t-1} + mP_{mo}(\beta_{o,t} - \beta_{o,t-1}) + mP_{mm}(\beta_{m,t} - \beta_{m,t-1})$$

where $G_{oo}$ and $G_{mm}$ are the additive genetic variances for the offspring and maternal effect traits, $m$ is the maternal effect coefficient (equal to the partial regression of the mother's phenotype on the offspring's phenotype holding genetic effects constant), $G_{mo}$ is the additive genetic covariance between the offspring and maternal effect traits, $\beta_{o,t}$ and $\beta_{o,t-1}$ are the selection gradients acting on the offspring trait at time t, $\beta_{m,t}$ and $\beta_{m,t-1}$ are the selection gradients acting on the maternal effect trait at time t, and $P_{mo}$ and $P_{mm}$ are the phenotypic covariance and variance (for conceptual diagram see Figure 1.1; Kirkpatrick & Lande, 1989). Assuming the trait of interest (z) is affected by maternal effects, an interesting outcome of the above equation is that maternal effects have the ability to accelerate, slow down, or even alter the direction of phenotypic change between generations (Kirkpatrick & Lande, 1989). For example, the response of a trait to selection may be slowed or reversed by maternal effects if the additive genetic covariance between offspring and maternal traits is negative in value. Furthermore, the equation also recognizes that maternal effects can influence phenotypic change in two ways: 1) maternal genetic effects; and 2) maternal environmental effects (environmental effects are a component of the maternal effect coefficient; Falconer & Mackay, 1996).

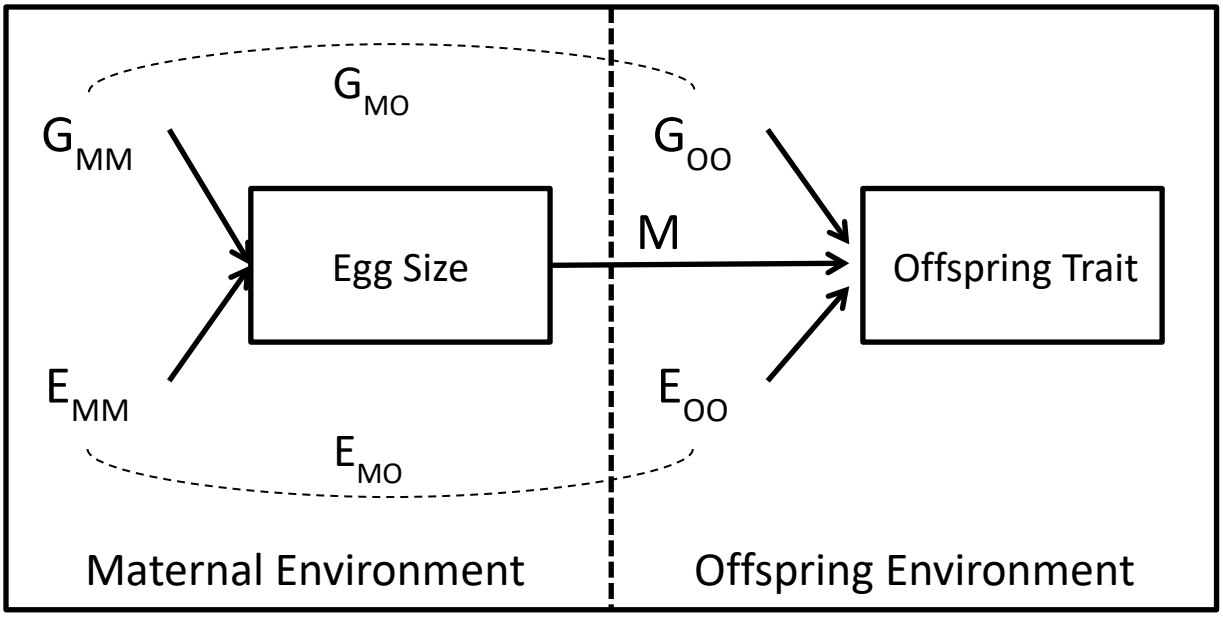


**Figure 1.1:** Conceptual diagram showing how a maternal effect trait (i.e. egg size) can influence the expression of an offspring trait. Additive genetic ($G_{MM}$) and environmental ($E_{MM}$) effects contribute to the expression of egg size within the maternal environment. Egg size ($G_{MM} + E_{MM}$) then contributes to the offspring phenotype as a maternal effect (M) in conjunction with additive genetic ($G_{OO}$) and environmental effects ($E_{OO}$) within the offspring environment. There is an additional effect of the covariance between the maternal additive genetic and environmental effects with those of the offspring ($G_{MO}$ and $E_{MO}$). The conceptual diagram is adapted from Wolf et al. (1998) and McAdam et al. (2014).

The way in which maternal genetic effects influence the inheritance of an offspring trait can best be understood in terms of heritability. Heritability is the proportion of phenotypic variation attributable to genetic effects (Falconer & Mackay, 1996; Lynch & Walsh, 1998). The narrow-sense heritability is the most common method used to estimate the heritability of a trait and it is calculated as the additive genetic variance of the focal trait divided by the total phenotypic variance. Willham (1972) extended the calculation of heritability to include maternal genetic effects using the following equation:

$$h^2 = (G_{oo} + \frac{1}{2} \cdot G_{mm} + \frac{3}{2} \cdot G_{mo})/V_z$$

where $G_{oo}$ and $G_{mm}$ are the additive genetic variances for the offspring and maternal traits (may not be a shared maternal-offspring trait), $G_{mo}$ is the additive genetic covariance between offspring and maternal traits, and $V_z$ is the total phenotypic variance in the offspring trait (for conceptual diagram see Figure 1.1). The maternal genetic effects incorporated into the total heritability equation are often termed indirect genetic effects and they can greatly affect the way phenotypes respond to selection (McAdam et al., 2014). For example, McAdam et al. (2002) found that the total heritability of juvenile growth in red squirrels (*Tamiasciurus hudsonicus*), which incorporated maternal care, was three-times larger than that of the narrow-sense heritability and more representative of the realized heritability calculated from extensive pedigrees (McAdam & Boutin, 2004). Similar results have been found for other species of mammals (Wilson, Kruuk, & Coltman, 2005; Wilson & Réale, 2006). Thus, maternal genetic effects are clearly important to consider when interpreting the heritability of a trait and that narrow-sense heritability estimates can overestimate or underestimate the heritability of a trait depending on its interaction with maternal effects (McAdam et al., 2002).

Maternal environmental effects are a form of nongenetic inheritance, whereby aspects of the maternal environment are transferred to the offspring generation through epigenetic variation, milk or yolk resources, hormones, immune factors, or behaviours (Bonduriansky, Crean, & Day, 2012). Maternal environmental effects are also called transgenerational maternal effects (TMEs). TMEs can have profound fitness

consequences for offspring and have been found to occur in a wide variety of taxa (Coslovsky & Richner, 2011; Franzke & Reinhold, 2013; Galloway & Etterson, 2007; Hafer, Ebil, Uller, & Pike, 2011; Helle, Koskela, & Mappes, 2012; Salinas & Munch, 2012; Shama et al., 2016; Shama, Strobel, Mark, & Wegner, 2014; Storm & Lima, 2010; Triggs & Knell, 2012; Zizzari, van Straalen, & Ellers, 2016). Though not a genetic effect, TMEs can affect the rate and direction of adaptation by influencing the way in which selection acts on an individual (Bonduriansky et al., 2012). Whether or not TMEs increase fitness depends on the nature of the maternal-offspring conflict and the environmental covariance between the maternal and offspring generations (Marshall & Uller, 2007; Rossiter, 1998). Maternal-offspring conflict is an important consideration because selection acting on offspring traits often acts to increase maternal fitness rather than offspring fitness and, from the offspring's point of view, TMEs may not improve fitness (Einum & Fleming, 2000a). Galloway and Etterson (2007) showed the adaptive benefit of TMEs using the herb, *Campanulastrum americanum*, which produced more seedlings of the annual life history type per mother when the offspring were reared in the same environment as the mother (open vs. understory). Given the diversity of life histories and maternal effects across species, much more research needs to be done to elucidate the many potential pathways through which TMEs can influence the evolution of offspring phenotypes.

The phenotypic and fitness consequences of maternal genetic and environmental effects depend on the offspring environment (Allen, Buckley, & Marshall, 2008; Donelson, Munday, & McCormick, 2009; Einum & Fleming, 1999; Ronget et al., 2018). For example, Einum and Fleming (1999) found that brown trout (*Salmo trutta*) hatched from large eggs grew faster in a semi-natural stream environment than those from small eggs; however, large eggs did not experience increased fitness within a benign hatchery environment. From a quantitative genetic perspective, the amount of phenotypic variation explained by maternal effects and additive genetic effects can vary across environments as well (Charmantier & Garant, 2005; Hoffmann & Merilä, 1999). Wilson et al. (2006) showed that the maternal genetic variation for birthweight in Soay sheep (*Ovis aries*) was negatively correlated with the quality of the offspring environment. However, quantitative genetic studies have often estimated parameters for only a single offspring

environment (e.g., Páez, Morrissey, Bernatchez, & Dodson, 2010; Perry, Audet, & Bernatchez, 2005; Pulido, Berthold, Mohr, & Querner, 2001) and, as a result, we have limited knowledge about how maternal effects vary across environmental conditions (Räsänen & Kruuk, 2007). Similarly, the majority of existing research has been conducted in a laboratory or semi-natural environment (reviewed for salmon by Carlson & Seamons, 2008) and there is a lack of studies investigating the influence of maternal effects on offspring phenotypes and performance in the wild.

By affecting evolution within populations, maternal effects can also contribute to the divergence of offspring traits among populations. Investigating the role of maternal effects in trait divergence among populations can reveal important information about offspring trait evolution that is difficult to gain from within population studies. First, looking at the patterns of population divergence and its association with maternal effect traits can help elucidate the way in which maternal effect traits shape offspring trait evolution under diverse environmental conditions (Badyaev et al., 2002; Räsänen, Laurila, & Merilä, 2003, 2005; Sinervo, 1990). For example, Räsänen et al. (2003) compared moor frog (*Rana arvalis*) populations from acidified and neutral environments and found that moor frogs had adapted to an acidified environment within 40 generations via a maternally mediated change in egg capsule composition. Second, phenotypic differences among populations derived from a common genetic ancestry can provide data on the magnitude and speed of evolution (Hendry & Kinnison, 1999). Most researchers are interested in genetic or total phenotypic divergence rates (Hendry & Kinnison, 1999; Kinnison & Hendry, 2001), and few have concentrated on the maternal component of divergence (Badyaev et al., 2002). Though studying evolution in the context of phenotypic divergence can provide valuable insights, there is still a lack of studies investigating phenotypic divergence with a focus on maternal effects across taxa.

For this dissertation, I used Chinook salmon (*Oncorhynchus tshawytscha*) to address several understudied questions about the evolutionary ecology of maternal effects: 1) how do maternal effects contribute to the divergence of offspring phenotypes among populations (i.e., contemporary evolution), 2) how do TMEs influence offspring

phenotypes across environmental conditions, and 3) how do maternal effects influence offspring survival in the natural environment?

## 1.2 Maternal Effects and Salmon

### 1.2.1 Maternal Effect Traits

Salmonids (hereafter salmon; Family: Salmonidae) are a good model organism because they have a relatively limited suite of maternal effect traits acting on offspring phenotypes. No maternal care is provided to offspring beyond a brief period of nest defence making egg quality the primary maternal effect. Egg quality can be broken down into two main traits: 1) egg size; and 2) egg nutrient content. Egg size exerts a strong influence on the expression of offspring traits during the early life history (embryogenesis-exogenous feeding) of salmon, including offspring length (Heath, Fox, & Heath, 1999), swim speed (Ojanguren, Reyes-Gavilán, & Braña, 1996), competitive ability (Cutts, Brembs, Metcalfe, & Taylor, 1999), growth (Einum & Fleming, 1999) and survival (Einum & Fleming, 2000b). How a female allocates resources (e.g., nutrients) to her eggs is determined by both genetic and environmental effects (Heath, Heath, Bryden, Johnson, & Fox, 2003; Jonsson, Jonsson, & Fleming, 1996; Kinnison, Unwin, Hendry, & Quinn, 2001). Variation in egg size among salmonid populations can be large (Beacham & Murray, 1993; Fleming & Gross, 1990; Quinn, Vøllestad, Peterson, & Gallucci, 2004), and this has been linked to differences in environmental selection factors such as gravel size (Quinn, Hendry, & Wetzel, 1995), food availability (Jonsson et al., 1996), and migratory distance (Kinnison et al., 2001). Egg size can also vary within populations due to female size (Beacham & Murray, 1985; Heath et al., 1999) and female growth rate (Morita et al., 1999). Because of its genetic basis, effect on offspring traits, and variability among salmon populations, egg size is an ideal maternal effect trait to use when trying to understand how maternal effects influence the contemporary evolution of offspring traits.

Egg nutrient content has also been shown to affect offspring phenotypes in salmon (Tocher, 2003; Wiegand, 1996). Nutrients are deposited in the egg in the weeks or months prior to spawning (Johnson, 2009; Lubzens, Young, Bobe, & Cerdà, 2010;

Tyler & Sumpter, 1996; Wiegand, 1996) and are primarily composed of lipid, protein, carbohydrates, and micronutrients (Brooks, Tyler, & Sumpter, 1997). Lipids represent the largest energy source during endogenous feeding and embryos with poor lipid reserves experience low survival and greater rates of developmental deformities (Srivastava & Brown, 1991). Furthermore, the fatty acids that make up the lipid reserve serve in a variety of structural and regulatory roles within cells (Sargent, Bell, McEvoy, Tocher, & Estevez, 1999; Wiegand, 1996). Of particular importance are the essential fatty acids from the n-3 and n-6 series that cannot be synthesized de novo, such as docosahexaenoic acid (DHA, 22:6n-3), eicosapentaenoic acid (EPA, 20:5n-3), and arachidonic acid (ARA, 20:4n-6; Sargent et al., 1999). Offspring with lipid stores low in essential FAs experience reduced growth, neural development, and survival (Copeman, Parrish, Brown, & Harel, 2002; Sargent, Bell, Bell, Henderson, & Tocher, 1995; Wiegand, 1996). Essential FAs, along with most others, are deposited in the egg with little to no modification directly from the maternal diet or indirectly from the diet via stored lipids in the somatic and visceral tissues (Iverson, 2009; Johnson, 2009; Wiegand, 1996). Thus, egg lipids primarily reflect the maternal diet during vitellogenesis and, as such, represent a useful maternal effect trait to study the influence of TMEs on offspring phenotypes.

### 1.2.2 Maternal Effects and Contemporary Evolution

Introduced salmon populations have been used extensively to study the contemporary evolution of adult and offspring phenotypes. Previous studies on introduced salmon populations have shown they that can undergo rapid adaptation (≥ 13 generations) in a variety of life history traits because of exposure to new selective regimes (Hendry, Hensleigh, & Reisenbichler, 1998; Jensen et al., 2008; Kinnison, Quinn, & Unwin, 2011; Kinnison et al., 2001; Koskinen, Haugen, & Primmer, 2002; Quinn, Unwin, & Kinnison, 2000; Unwin, Quinn, Kinnison, & Boustead, 2000). For example, Chinook salmon populations introduced to New Zealand (~30 generations) have undergone phenotypic divergence in juvenile growth (Unwin et al., 2000), adult size and growth profiles (Kinnison et al., 2011), timing of return migration and spawning (Quinn et al., 2000), and egg size and fecundity (Kinnison et al., 2001). Thus far, the focus has been on identifying the presence of phenotypic divergence and establishing

whether there is a likely additive genetic basis (Hendry, 2001; Quinn, Kinnison, & Unwin, 2001). As a result, maternal effects have generally been treated as a source of confounding environmental variance and not as a potential contributor to evolutionary change.

The evolutionary significance of a maternal effect trait can be inferred from the amount of offspring trait variation that is explained by the maternal effect trait within and among populations. For salmon, egg size is an important maternal effect trait whose effect on phenotypic variation within and among populations has been poorly quantified. Within populations, the variance in offspring traits explained by egg size has generally been quantified using a simple linear regression (Heath & Blouw, 1998), without accounting for the confounding effects of the breeding design (Burt, Hinch, & Patterson, 2011). Meanwhile, quantitative genetic studies that do account for breeding design have focused on quantifying the variance attributable to maternal identity and not specific maternal effect traits (Falica, Lehnert, Pitcher, Heath, & Higgs, 2017; Heath et al., 1999; Houde et al., 2013; Páez, Morrissey, Bernatchez, & Dodson, 2010). Among populations, the variation in offspring traits explained by egg size has mostly been qualitatively assessed using statistical inference (Hendry et al., 1998; Koskinen et al., 2002). Thus far, no studies have quantified both the within and among population variation in offspring traits explained by egg size, while also accounting for other sources of phenotypic variation (i.e., breeding design). In chapter 2, I use a model comparison approach to quantify the within and among population variation in offspring traits attributable to egg size.

### 1.2.3 Transgenerational Maternal Effects

TMEs on salmon offspring have been demonstrated in a variety of ways. Broadly, maternal rearing environment or life history strategy has been shown to affect offspring growth and survival in salmonids (Burton, McKelvey, Stewart, Armstrong, & Metcalfe, 2013; Evans, Wilke, O'Reilly, & Fleming, 2014; Liberoff et al., 2014). For example, Evans et al. (2014) reared Atlantic salmon broodstock in captivity and natural river conditions and found that offspring spawned from mothers reared in natural conditions had greater survival in stream than offspring from captive reared mothers. Such studies

have shown an effect of maternal rearing environment on offspring phenotype and performance, but they do not link the two generations via a specific maternal effect trait.

Egg size and nutrients are maternal effect traits that can link the maternal environment to the offspring environment. Both maternal origin (i.e., hatchery vs wild; Fleming, Lamberg, & Jonsson, 1997; Jonsson et al., 1996) and temperature (Braun, Patterson, & Reynolds, 2013; Jonsson & Jonsson, 2016) have been shown to affect the way in which females invest into reproduction and egg size. Environmentally induced changes in egg size then influence offspring size because of the positive egg size-offspring size relationship (Braun et al., 2013). Unlike egg size, egg nutrients have a less predictable effect on offspring traits. Threshold levels for essential fatty acids (FAs) and the response of offspring traits to FA composition vary among species and populations (Glencross, 2009; Tocher, 2003, 2010). Furthermore, most of the research on fatty acids (FAs) and salmon has been derived from an aquaculture setting using simplified diets (Glencross, 2009), and it is unclear how natural variation in fatty acids may impact offspring development.

Natural variation in the FA composition of salmon eggs stems from variation in the available forage base (Ashton, Farkvam, & March, 1993; Pickova, Kiessling, Pettersson, & Dutta, 1999). Such variation in egg fatty acid composition has been shown to affect rates of early life mortality in salmon (Czesny, Dettmers, Rinchard, & Dabrowski, 2009; Czesny et al., 2012; Pickova et al., 1999). For example, Czesny et al. (2009) found that rates of pre- and post-hatch mortality in lake trout (*Salvelinus namaycush*) were associated with a variety of FAs derived from both neutral lipids and phospholipids. Egg FA content is likely to affect other offspring phenotypes, such as growth, because of its role in energy production and cellular function (Tocher, 2003). How egg FA content influences offspring phenotypes will depend on temperature, which affects both the structural and metabolic functioning of FAs (Hazel, 1984, 1995; Laurel, Copeman, & Parrish, 2012; March, 1993; Mueller et al., 2015; Ng, Sigholt, & Gordon Bell, 2004; Robertson & Hazel, 1997). However, most studies of egg FA composition and offspring survival/development have used a single rearing environment (Czesny et al., 2009; Czesny et al., 2012; Pickova et al., 1999), which does not provide an accurate

picture of how FA composition may influence offspring phenotypes in the wild. In Chapter 3, I rear embryos from three different populations under three different thermal regimes to determine how natural variation in egg FA composition affects offspring development and growth across a thermal gradient.

### 1.2.4 Maternal Effects and In-Situ Survival

Significant mortality is often incurred during the early life history of salmon (Houde, 1989, 1994; Leggett & Deblois, 1994; Pepin, 1991) and understanding the factors that influence early life survival (fertilization – exogenous feeding) is important for the effective management of salmon populations (Greene & Beechie, 2004; Kareiva, Marvier, & McClure, 2000). The factors that influence early life survival in salmon can be categorized as extrinsic factors (i.e., environmental) or intrinsic factors (i.e., maternal and genetic effects). Both hatchery and in-situ studies have been used to identify extrinsic factors important for in-situ survival during incubation, including substrate composition (Chapman, 1988; Greig, Sear, & Carling, 2005; Jensen et al., 2009; Witzel & MacCrimmon, 1981), dissolved oxygen (Greig et al., 2007; Malcolm et al., 2011; Malcolm et al., 2003), scour (Cunjak & Therrien, 1998; Gauthey et al., 2017), and temperature (Pepin, 1991; Richter & Kolmes, 2005). Studies of intrinsic factors have identified egg size as an important intrinsic effect that can influence survival and development through interactions with dissolved oxygen (Einum, Hendry, & Fleming, 2002), temperature (Régnier, Bolliet, Gaudin, & Labonne, 2013), and substrate composition (Rollinson & Hutchings, 2011). Unlike extrinsic factors, most of what we know about egg size, maternal effects, and early life survival has been derived in a hatchery, where selection is often weak and not reflective of a natural environment.

In-situ studies of early life history survival rarely incorporate intrinsic effects (Einum & Fleming, 2000a; Gauthey et al., 2017; Johnson, Roni, & Pess, 2012; Roni et al., 2016). Egg size effects on early life survival appear to be more complex in-situ and vary from no effect to a positive relationship depending on the study population (Einum & Fleming, 2000a; Gauthey et al., 2017). Furthermore, interactions between egg size and redd (i.e., nest) environmental variables have not been detected in-situ (Gauthey et al., 2017). Roni et al. (2016) tracked family-level survival in-situ and found that parentage

has a significant influence on early life survival; however, the breeding design employed did not allow genetic and maternal effects to be estimated. Based on the available in-situ studies, there are several outstanding questions regarding intrinsic effects and early life survival: 1) why do egg size effects vary among populations in the wild; 2) how do maternal and genetic effects contribute to early life survival in the wild; and 3) are hatchery derived relationships between intrinsic effects and early life survival transferable to the wild? To answer these questions, the effects of egg size, parentage (maternal and genetic effects), and environmental conditions on early life survival need to be quantified in the wild across several populations because each salmonid population has a complex mix of environmental selection factors. Furthermore, the transferability of hatchery-based studies can only be assessed by rearing related individuals in a hatchery and natural setting. In Chapter 4, I address these outstanding questions by quantifying the effects of egg size, parentage, and environmental conditions on early life survival in both the hatchery and wild using three introduced Chinook salmon populations.

## 1.3 Study System: Laurentian Great Lakes Chinook Salmon

The introduction of Chinook salmon (*Oncorhynchus tshawytscha*) to the Laurentian Great Lakes (hereafter Great Lakes) provides a novel opportunity to investigate the evolutionary ecology of maternal effects in post-colonizing salmonids. Chinook salmon were first introduced to the Great Lakes in the 1960's by the transfer of embryos from the Green River, Washington in an effort to control alewife (*Alosa pseudoharengus*) populations and expand the recreational fishery (Crawford, 2001; Parsons, 1973; Peck, Jones, MacCallum, & Schram, 1999; Weeder, Marshall, & Epifanio, 2005). Since then, Chinook salmon have colonized tributaries throughout the Great Lakes and there are now high rates of natural reproduction in several Great Lakes (Connerton, Murry, Ringler, & Stewart, 2009; Johnson, DeWitt, & Gonder, 2010). Tributary environments can vary considerably within and among the Great Lakes and, given the strong natal philopatry exhibited by salmon, it is likely that naturalized Chinook salmon populations have begun the process of local adaptation and population divergence. However, relatively little is known about the evolution of these populations.

Weeder et al. (2005) used 18 allozyme loci to determine if introduced Lake Michigan Chinook salmon populations have diverged genetically and found that there was little evidence of genetic heterogeneity among the seven study populations. Using different genetic markers, Suk et al. (2012) found evidence of genetic differentiation among Lake Huron Chinook salmon populations using nine microsatellite loci from 13 naturalized and 2 hatchery populations. Because selection acts on phenotypes, random or neutral genetic markers may take longer to diverge relative to phenotypes or functional genetic markers (Reed & Frankham, 2001). Purcell et al. (2014, 2008) showed that resistance to bacterial kidney disease (*Renibacterium salmoninarum*) diverged between an introduced Lake Michigan population and the Green River, Washington progenitor population; however, this divergence did not appear to have a genetic basis. Taken together, introduced Great Lakes Chinook salmon populations appear to be in the early stages of population divergence and, thus far, no studies have investigated whether there is evidence of local adaptation and population divergence in early life history traits.

## 1.4 Dissertation Structure

My dissertation addresses three primary research questions related to the evolutionary ecology of maternal effects in salmon: 1) what is the effect of egg size on the patterns of phenotypic divergence of offspring traits among introduced Chinook salmon populations, 2) how does within and among population variation in egg fatty acid content influence the expression of offspring traits across rearing temperatures, and 3) how does egg size influence the survival of Chinook salmon in a natural setting?

In Chapter 2, I tested the hypothesis that egg size would contribute significantly to the within and among population variation in offspring traits using three introduced Great Lakes Chinook salmon populations. Because maternal effects are often context dependent, I also tested the hypothesis that the influence of egg size on offspring traits would depend on the thermal environment. To test these hypotheses, I collected gametes from three introduced Chinook salmon populations (Credit, Pine, and Sydenham Rivers), crossed gametes from each population using a paternal half-sib breeding design, reared them in a common garden hatchery study at 6.5°C, 9.4°C, and 15.2°C, and measured a variety of offspring traits. Egg size explained most of the among population variation in

offspring traits; however, the egg size effect decreased with an increase in temperature, which indicated other sources of variation, such as genetic, are important at high temperatures. I also found that egg size explained much of the maternal variance in offspring traits within populations, which suggests that egg size is the primary maternal effect trait acting on offspring phenotypes. Egg size made a significant contribution to both the among and within population variation in offspring traits and represents an important pathway through which offspring phenotypes can evolve on contemporary timescales.

In Chapter 3, I tested the hypothesis that variation in egg fatty acid and proximate composition affect the expression of offspring phenotypes during the endogenous feeding stage at different temperatures. To do this, I reared embryos from three introduced Great Lakes Chinook salmon populations in a common garden hatchery study at 6.5°C, 9.4°C, and 15.2°C. During development, I measured hatch length, swim-up length, hatch to swim-up growth, and survival. I found that the relative quantity of lipid, lean mass, and water was similar among the populations, whereas the fatty acid composition differed. After controlling for egg mass, egg fatty acid and proximate composition influenced hatch length, swim-up length, and hatch to swim-up growth. Furthermore, the direction and magnitude of these egg quality effects depended on population and temperature treatment. Overall, these results demonstrate that natural variation in egg nutrient composition has transgenerational effects on offspring development under varying thermal conditions.

In Chapter 4, I addressed four research objectives related to maternal effects and early life history survival: 1) assess the effect of egg mass and parental effects on the hatching success of Chinook salmon in the wild; 2) assess the influence of redd gravel composition, a primary extrinsic effect, and its interaction with egg mass on hatching success in the wild; 3) determine whether egg mass – survival relationships have population-level consequences in the wild; 4) determine if results from hatchery studies translate to the wild. I did this by collecting gametes from three Chinook salmon populations and reared the resulting embryos from fertilization to 15 days post hatch in the hatchery and wild. I found that egg mass was significantly related to in-situ hatching

success in the Credit River (non-linear) and Sydenham (linear), whereas there was no relationship in the Pine River. Furthermore, maternal identity explained a significant among of the variation in hatching success for the Pine and Sydenham River. Within populations, no interaction was detected between egg mass and gravel composition; however, an interaction was present when the data were pooled among populations. I also found that egg mass and quantitative genetic parameter estimates were different between the hatchery and wild indicating that hatchery-based observations cannot be transferred to the wild. Finally, I used the in-situ survival data from the Credit and Sydenham Rivers along with published data in a simulation analysis, which showed that both linear and non-linear egg mass – survival relationships can greatly affect the number of alevins produced by a population depending on where the population egg mass distribution falls along an egg mass selection gradient. Overall, egg mass can greatly influence hatching success in the wild and selection acting on egg mass can have population-level consequences by affecting the production of alevins.

In my final chapter (Chapter 5), I synthesize the primary findings from each data chapter and discuss how they further our understanding of maternal effects and the contemporary evolution of salmon. I also highlight areas of future research and provide some potential management implications of my work.

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# 2 Egg size and the adaptive capacity of early life history traits in Chinook salmon (*Oncorhynchus tshawytscha*)[1]

## 2.1 Introduction

Temperature has a direct effect on the rate of biological reactions within the body of ectotherms (Gillooly, Brown, West, Savage, & Charnov, 2001; Huey & Kingsolver, 1989) and alterations to environmental temperature regimes, such as those predicted for climate change, can have a dramatic impact on the development, fitness, and lifespan of these organisms (Andrews & Schwarzkopf, 2012; Clusella-Trullas, Blackburn, & Chown, 2011; Fry, 1967; Munch & Salinas, 2009; Paaijmans et al., 2013; Wood & McDonald, 1997). Temperature variation does not necessarily affect all life stages equally and the early life history stages are often the most vulnerable because offspring tend to have a low tolerance for temperature variation (Rombough, 1997; Xu & Ji, 2006) and a reduced capacity to behaviourally thermoregulate (Quinn, 2005). Furthermore, offspring tend to experience strong selection pressures, such as size-selective mortality (Elliott, 1990; Sogard, 1997), and a temperature mediated shift in offspring phenotype or habitat can reduce offspring fitness (Crozier et al., 2008; Ficke, Myrick, & Hansen, 2007; Massot, Clobert, & Ferrière, 2008; Visser & Both, 2005). A reduction in survival during early life can have a strong negative effect on recruitment and threaten the persistence of a population (Kareiva, Marvier, & McClure, 2000; Venturelli et al., 2010; Zabel, Scheuerell, McClure, & Williams, 2006). Populations facing such a predicament will need to adapt by shifting offspring phenotypes on ecological timescales. To understand the adaptive capacity of offspring traits, we need to know the sources of phenotypic variation underlying the traits and how the contribution of these sources is influenced by temperature.

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[1] Thorn, M.W., & Morbey, Y.E. (2018). Egg size and the adaptive capacity of early life history traits in Chinook salmon (*Oncorhynchus tshawytscha*). Evolutionary Applications 11: 205-219.

In fishes, egg size has been shown to affect the variation in offspring phenotypes, whereby there is a positive relationship between egg size and offspring size (Chambers & Leggett, 1996; Heath & Blouw, 1998). Large juveniles often experience increased competitive ability (Cutts, Brembs, Metcalfe, & Taylor, 1999), growth (Einum & Fleming, 1999), swimming performance (Ojanguren, Reyes-Gavilán, & Braña, 1996), and survival (Sogard, 1997). However, any developmental and fitness advantages of large egg size are context-dependent and can vary across environmental gradients (temperature: Beacham & Murray, 1985; Régnier, Bolliet, Gaudin, & Labonne, 2013; habitat: Einum & Fleming, 1999; food resources: Segers & Taborsky, 2011). For example, Beacham and Murray (1985) found that the size of chum salmon (*Oncorhynchus keta*) juveniles was positively related to egg size at 4°C and 8°C, whereas there was no relationship at 12°C (i.e., large and small eggs produce similar sized juveniles). The phenotypic variation explained by egg size has often been quantified using a regression between egg size and an offspring trait, which provides an estimation of the total variation explained by egg size (i.e., $R^2$; Heath & Blouw, 1998) and does not partition the variation explained among and within populations. Furthermore, few studies have controlled for the breeding design employed, which may result in the inaccurate estimation of the egg size effect (Burt, Hinch, & Patterson, 2011). Given the influence egg size has on offspring phenotypes, quantifying the contribution of egg size to the among and within population variation is crucial for our understanding of early life history trait evolution.

Quantitative genetic studies provide information on the genetic, maternal, and environmental sources of phenotypic variation within a population, which is necessary to elucidate the potential pathways through which populations may respond to a change in temperature (Lynch & Walsh, 1998). Quantitative genetic studies of early life history traits have shown that these traits are largely influenced by maternal rather than genetic effects (Falica, Lehnert, Pitcher, Heath, & Higgs, 2017; Heath, Fox, & Heath, 1999; Houde, Wilson, & Neff, 2013; Kinnison, Unwin, Hershberger, & Quinn, 1998; Páez, Morrissey, Bernatchez, & Dodson, 2010; Pitcher & Neff, 2007). Often, these studies quantify the maternal effect as the proportion of phenotypic variation explained by dam identity, which does not provide information on the maternal effect traits that contribute

to the overall maternal effect (McAdam, Garant, & Wilson, 2014). Haugen and Vøllestad (2000) found that egg size does make a significant contribution to the maternal variation in grayling (*Thymallus thymallus*) early life history traits, but they were unable to quantify the amount of maternal variation explained by egg size. Another limitation of many quantitative genetic studies is the use of a single thermal environment (Burt et al., 2011). Natural environments are rarely static and the rearing environment can greatly influence the estimation of quantitative genetic parameters (Carlson & Seamons, 2008; Charmantier & Garant, 2005; Hoffmann & Merilä, 1999). As a result, the contribution of egg size to the within population variation in offspring traits may vary across a thermal gradient.

Quantifying the among population variation in offspring traits explained by egg size can provide information about the capacity of egg size to alter these traits. Frequently, studies of contemporary evolution are specifically interested in genetic differences among populations and merely control for egg size effects when comparing traits among populations (Hendry, Hensleigh, & Reisenbichler, 1998; Jensen et al., 2008; Kinnison et al., 1998). Those that are interested in egg size often use statistical inference or qualitative assessments to determine how egg size contributes to the among population variation in offspring traits (Ghani, Izza, Herczeg, & Merilä, 2012; Jones & Closs, 2016; Koskinen, Haugen, & Primmer, 2002). Using a different approach, Aykanat, Bryden, and Heath (2012) crossed males and females from several Chinook salmon populations (*Oncorhynchus tshawytscha*) in a factorial breeding design and found that among population maternal effects, but not specifically egg size, explained most of the observed population differences in offspring traits. Though egg size has commonly been implicated in the among population variation in offspring traits, a measure of effect size is generally lacking and is required to fully understand how egg size can contribute to population divergence.

The term phenotypic divergence can have two meanings depending on the nature of the experimental design. Allochronic studies compare phenotypic traits of the same population between two or more time periods, which allows for the measurement of evolutionary rates (i.e., change within a population over time; Hendry & Kinnison, 1999).

Synchronic studies compare phenotypic traits among populations that share a common ancestral source at some point on the past, which allows for the calculation of divergences rates (i.e., change among populations over time; Hendry & Kinnison, 1999). For the current study, I refer to phenotypic divergence within the context of the latter study design and infer evolutionary change among populations that share a common ancestral population.

In the Laurentian Great Lakes, Chinook salmon populations were first introduced in the late 1960s from the Green River, Washington (Parsons, 1973; Weeder, Marshall, & Epifanio, 2005). This introduction represents one of the largest ecosystem manipulations in the world. Since their introduction, Chinook salmon have colonized tributaries throughout the Great Lakes and there is now evidence of high natural reproduction (Connerton, Murry, Ringler, & Stewart, 2009; Johnson, DeWitt, & Gonder, 2010). There is also evidence of weak genetic structuring among the populations (Suk, Neff, Quach, & Morbey, 2012) suggesting that there is potential for phenotypic divergence of early life history traits. For this study, I used introduced Great Lakes Chinook salmon populations to test several hypotheses: 1) divergence in early life history traits among introduced Chinook salmon populations will be largely mediated by variation in egg size; 2) egg size will also influence the estimation of quantitative genetic parameters (i.e., within population variation); and 3) the variance explained by egg size, both among and within populations, will depend on the rearing temperature of the offspring. I reared progeny from three Great Lakes Chinook salmon populations in a common garden hatchery experiment under three different temperature regimes, and measured a variety of fitness-related early life history traits. I then used a model comparison approach, whereby we compared models before and after including egg size, to quantify the variation among and within populations that is explained by egg size across the three temperature treatments.

## 2.2 Materials and Methods

*Study Populations*

The populations used in this study were from the Credit River (CR), Pine River (PR), and Sydenham River (SR; Figure 2.1). Chinook salmon were introduced to Lake

Huron by the Michigan Department of Natural Resources starting in 1968 using embryos from the Green River, Washington (Parsons, 1973; Weeder et al., 2005). Stray Chinook salmon from Michigan stocking operations eventually colonized the PR and SR in southern Georgian Bay, Lake Huron in ~ 1980 (Kerr & Perron, 1986; Suk et al., 2012). Chinook salmon were then introduced to Lake Ontario in 1969 via the Little Salmon River, New York using a combination of Chinook salmon from established populations in Michigan (probably from Lake Huron) and embryos sent from the Green River, Washington (Donaldson & Timothy, 1983). In 1982, the Ontario Ministry of Natural Resources and Forestry initiated a Chinook salmon stocking program in the CR using previously established Lake Ontario Chinook salmon populations (Daniels & LeTendre, 1987; FWS/GLFC, 2010). Therefore, all the populations used in this study descended from the Green River, Washington population. The populations have been separated for ~ 30 years, which translates into ~ 10 generations using an estimated generation time of 3 years (Haring, Johnston, Wiegand, Fisk, & Pitcher, 2016; Suk et al., 2012).

The migration distance and timing differ among the study populations, whereas the rivers have similar thermal profiles. The SR has the shortest migration distance of ~7 kilometers (km), followed by the CR at ~ 14 km, and the PR has the longest migration of > 100 km. The PR population arrives at their spawning grounds as early as mid-August, whereas the CR and SR typically arrive in late-September (Gerson, Marklevitz, & Morbey, 2016; M. Thorn personal observation). Thermal profiles are similar among the rivers, with mean (± SE) water temperature between mid-October 2010 and May 2011 of 2.9°C ± 0.30, 2.5°C ± 0.21, and 3.1°C ± 0.23 for the CR, PR, and SR, respectively (Appendix A.1).

*Gamete Collection*

Chinook salmon were collected at the Streetsville Dam in the CR using electrofishing (43°34'39.58"N, 79°42'8.57"W), at the Mill Street Dam in the SR using a fish trap built into the dam (44°33'34.36"N, 80°56'39.49"W), and at the PR using a combination of dip and seine nets (44°13'10.12"N, 79°57'24.84"W). Because of differences among the populations in run timing, adults were collected in the CR on 01

October 2012, in the PR from 19-27 September 2012, and in the SR from 22 September – 06 October, 2012. When an adult was captured, it was anesthetized by immersing it in a clove oil solution (20 mg/L), measured for fork length and mass, and checked for sexual maturity. If the individual was found to be sexually-mature, a sample of eggs or sperm was collected by gently massaging the abdomen. Approximately 500 eggs and a few milliliters of milt were taken from each female and male, respectively. Visually unhealthy salmon were not used. All collected fish were released once gamete sampling was complete. Egg and milt samples were stored in a cooler (~ 4°C) and transported directly to the Western University experimental hatchery for fertilization within 8 hours of collection.

*Hatchery Experiment*

Eggs from each population were partitioned into separate egg containers (40 eggs per container; 6 cm diameter x 5 cm height) according to maternal origin (6 containers per female) and then fertilized using a nested full-sib, half-sib breeding design (1 male x 2 females; Lynch & Walsh, 1998). The fertilization procedure yielded 20 CR (10 males x 20 females), 26 PR (13 males x 26 females), and 22 SR families (11 males x 22 females). Two egg containers from each family (80 fertilized eggs) were placed in upwelling incubation trays at a mean temperature (°C ± S.D.) of 6.5 ± 0.8, 9.4 ± 0.3, and 15.2 ± 0.02 (i.e., two containers from each female at each temperature). These temperatures were chosen because they represent the range of temperatures the three populations experience in the wild during incubation (Appendix A.1). The 15.2°C treatment reflects the warm water temperatures experienced by embryos early during incubation and later into the summer as free feeding juveniles (~June). The 9.4°C treatment is a mid-range temperature that is close to the optimum growth temperature of Chinook salmon (Richter & Kolmes, 2005). The 6.5°C treatment was the lowest possible temperature we could achieve in the hatchery and reflects the lower range of temperatures these populations can experience during incubation. A sample of 25 eggs from each female was also retained and measured for egg diameter using handheld calipers to the nearest 0.1 mm. The developing embryos were checked daily and all dead/unfertilized eggs were removed. The removed eggs were stored in Stockard's solution and later checked for evidence of

embryonic development (Boyd, Oldenburg, & McMichael, 2010). This allowed for the calculation of fertilization success and embryo mortality for each egg container. After hatch, the developing alevins remained in the egg containers until they had reached the swim-up stage, which is when the fish have absorbed the yolk sac, are neutrally buoyant, and begun free feeding. The fish were then transferred family-wise to larger containers (10.5 cm diameter x 35 cm height) suspended in large recirculating tanks set at the same thermal regimes as the vertical incubators the families originated from. At this time, one egg container per family at each temperature was chosen at random and the individuals euthanized for swim-up measurements. The transferred fish were fed *ad libitum* in the large containers until the termination of the experiment at 300 degree days post hatch, where the remaining individuals were euthanized for juvenile measurements. Degree days were calculated as the cumulative sum of daily mean temperatures. No fish in the warm treatment were sampled at the juvenile stage because of a large die off that occurred prior to the termination of the experiment. All procedures in this study were approved by the Western University Animal Use Subcommittee.

*Trait Measurements*

A variety of fitness-related early life history traits were measured during the experiment: hatch length, yolk sac volume, yolk-sac conversion efficiency, swim-up length, hatch to swim-up growth rate, juvenile length, and swim-up to juvenile growth rate. All length measurements were taken from the anterior tip of the snout to the posterior tip of the hypural plate (i.e., standard length). Hatch length and yolk sac volume were measured from digital photographs taken of each family next to a ruler in a petri dish with water using the computer program imageJ (http://imagej.nih.gov/ij/). Yolk sac volume was estimated as:

$$V = (\pi/6) \times L \times H^2$$

where L is the yolk sac length (mm) and H is the yolk sac height (mm; Blaxter & Hempel, 1963). Yolk sac conversion efficiency was estimated as:

$$Y = (L_S - L_H) / V$$

where $L_S$ is swim-up length (mm), $L_H$ is hatch length (mm), and V is the yolk-sac volume ($mm^3$; Fraser et al., 2010). Swim-up and juvenile length were measured using hand held calipers to the nearest 0.1 mm. Growth rates were calculated as:

$$G = (L_2 - L_1) / \Delta D$$

where $L_2$ is the length of the later life-history stage (mm), $L_1$ is the length of the earlier life-history stage (mm), and $\Delta D$ is the growing degree days between the two life-history stages (Jensen et al., 2008). The growing degree days were measured as the cumulative sum of mean daily temperature up to a given time period (Jensen et al., 2008). Wet mass was measured using a Mettler-Toledo AL204 analytical balance to the nearest 0.001 g. The number of offspring measured for a given trait varied per family and population depending on mortality at each temperature and stage of development. The sample size information for each trait/population/temperature combination is provided in Appendix A.2. All phenotypic data used in this study are archived in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.r4ps0

*Egg Size Comparison Among Populations*

All analyses were conducted using the R statistical computing environment (version 3.2.5; R Core Team, 2016). Egg diameter was compared among populations using one-way analysis of variance (ANOVA) and an analysis of covariance (ANCOVA) with female fork length as a covariate followed by post-hoc Tukey tests. Female length was included in the analysis because egg size has been found to be positively related to female body size (van den Berghe & Gross, 1989). The fork length x population interaction was found to be non-significant ($P > 0.05$) and was dropped from the analysis.

*Egg Size and Multivariate Trait Comparisons*

To assess the differences in early life history traits among populations, I used non-metric multidimensional scaling (nMDS) ordination based on a Euclidean distance matrix and a permutational multivariate analysis of variance (PERMANOVA) using the vegan package in R (Oksanen et al., 2016). I used a multivariate approach to evaluate population differences because the analysis incorporates all the traits and provides a more

holistic picture relative to comparing individual traits. nMDS was selected instead of an eigenvector based method, such as principal components analysis, because I was interested in using all the variance in the early life history data to visualize the distance among populations and not just part of the variance associated with a subset of gradients (Paliy & Shankar, 2016). A Euclidean distance matrix was created using all the morphological and growth-related traits measured at a given temperature treatment. The trait data was standardized into z-scores prior to calculating the Euclidean distance matrix. An nMDS ordination was considered acceptable if the stress value was $\leq 15$ (Clarke, 1993). A primary assumption of the PERMANOVA test is the homogeneity of dispersion and I tested this assumption using a multivariate version of Levene's test (vegan function; Oksanen et al., 2016). I found that none of the trait matrices violated this assumption ($P > 0.05$). The PERMANOVA was first run on the full early life-history trait matrix using population as a fixed effect to see if there was an overall effect of population. If the population effect was significant, I repeated the PERMANOVA analysis on all pairwise population combinations to determine which populations were different. The analysis was run for each temperature separately.

I then used a Mantel test to determine if there was a correlation between the early life-history trait distance matrix and an egg size distance matrix (both Euclidean distance matrices). The significance of the Mantel test was determined by permuting one of the distance matrices 999 times (vegan function; Oksanen et al., 2016). I ran a separate Mantel test for each temperature treatment.

*Egg Size and Among Population Variation*

I used a model comparison approach to evaluate the effects of egg size on the among population variation in early life history traits. I did this by comparing models before and after controlling for egg size using linear mixed models. Length and volume trait data were collected at the individual-level, whereas the growth traits were derived measures at the family-level. As a result, I had to specify different models for the individual- and family-level traits. The linear mixed models used to compare the individual-level traits before (1) and after (2) controlling for egg size were:

$$z_{ijklm} = \mu + P_i + V_{S_{ij}} + V_{D_{ijk}} + V_{C_{ijkl}} + V_{E_{ijklm}} \quad (1)$$

$$z_{ijklm} = \mu + P_i + EG_k + P\ x\ EG + V_{S_{ij}} + V_{D_{ijk}} + V_{C_{ijkl}} + V_{E_{ijklm}} \quad (2)$$

where $z_{ijklm}$ is the phenotype of the *m*th offspring of the *i*th population, *j*th sire, *k*th dam, and *l*th container, $P$ is the fixed effect of population, $EG$ is the egg size covariate, $P\ x\ EG$ is the interaction between population and egg size, $V_{S_{ij}}$ is the random effect of the sire, $V_{D_{ijk}}$ the random effect of the dam nested within sire, $V_{C_{ijkl}}$ the random effect of container nested within sire and dam, and $V_{E_{ijklm}}$ is the environmental variation (i.e., residual error). Container was included as a random effect for hatch length and yolk sac volume to account for variation among replicates of each family. These replicate containers were split at the swim-up stage for sampling/further rearing, which resulted in a single cup being used for swim-up and juvenile measurements (i.e., cup not included in models for these traits). For the family-level growth traits, the dam and container effects could not be estimated, and I controlled for among family variation by including sire as a random effect in the linear mixed models. The significance of the fixed effects in the linear mixed models was assessed using a Wald test implemented in the car package (Fox & Weisberg, 2011). I dropped the interaction term from the egg size models if it was found to be non-significant. For models with a significant population effect, traits were compared between populations using pair-wise post hoc comparisons in the R package lsmeans (Lenth, 2016). I did not run a model for each trait with temperature as a fixed effect because the presence of population x temperature and egg size x temperature interactions prevented us from isolating the variance explained by population and egg size. Therefore, I ran the models separately at each temperature and then compared the results across the temperature treatments.

I estimated the variation explained by the individual fixed effects, the random effects, and the full model for the linear mixed models before and after including egg size as a covariate using the approach described by Nakagawa and Schielzeth (2013). Briefly, the fixed effect variation was calculated for the population and egg size effects separately by multiplying the design matrix of a given fixed effect by the vector of estimates for the

same fixed effect, and then taking the variance of the product. Random effect variation was quantified as the sum of the variation explained by all the random effects in the model (i.e., sire, dam and cup variation). The variation accounted for by the full model was calculated as the sum of the fixed and random effect variation. I presented the variation explained by the fixed effects, random effects, and full model as a proportion of the total variation, which was equal to the sum of the fixed effect, random effect, and residual variation. I excluded any traits that had a population x egg size interaction or did not have a relationship with egg size because the variance of population and egg size could not be separated or estimated. All the linear mixed models were fit using the lme4 package (Bates, Mächler, Bolker, & Walker, 2015).

*Egg Size and Genetic Architecture*

For individual-level traits, I also used a model comparison approach to quantify the influence of egg size on quantitative parameters (McAdam et al., 2014). Using the models described above, I compared the sire variance, dam variance, heritability, and maternal effects from linear mixed models before and after including egg size as a covariate for each trait. The heritability was calculated as four times $V_S$ divided by the total phenotypic variance ($V_P = V_S + V_D + V_C + V_E$) because $V_S$ accounts for ¼ of the additive genetic variance when using a half-sib, full-sib breeding design (Falconer & Mackay, 1996). Maternal effects were calculated by subtracting $V_S$ from $V_D$, and then dividing by the total phenotypic variance (Lynch & Walsh, 1998). The linear mixed models were fit using the nlme package (Pinheiro, Bates, DebRoy, & Sarkar, 2016). The significance of the variance components was assessed using a simulation-based restricted likelihood ratio test implemented using the RLRsim package in R (Scheipl, Greven, & Küchenhoff, 2008).

Bootstrap 95% confidence intervals (CIs) for the quantitative genetic parameters in the linear mixed models were estimated by resampling individuals within a family with replacement until the original sample size was replicated (Lynch & Walsh, 1998). Resampling of individuals was done to account for within-family variation, which allows for an unbiased calculation of the total phenotypic variance and prevents the

overestimation of genetic effects (Puurtinen, Ketola, & Kotiaho, 2009). The resampled dataset was then used to estimate the variance components as well as the maternal effect and heritability. The resampling procedure was repeated for 5000 iterations. Bias corrected and accelerated bootstrap confidence intervals were then calculated for each variance component, the maternal effect, and the heritability (Efron, 1987). The confidence intervals were used to determine if there was a significant change in the parameters before and after including egg size as a covariate by assessing the overlap in the confidence intervals (i.e., no overlap = significant difference).

*Egg Size and Divergence Rates*

The pairwise phenotypic divergence rates for egg size and the early life history traits between the populations were calculated using Haldanes (Gingerich, 1993). The Haldane is calculated as:

$$h = \frac{\left(\frac{\overline{x_2}}{s_p}\right) - \left(\frac{\overline{x_1}}{s_p}\right)}{g}$$

where $\overline{x_1}$ and $\overline{x_2}$ are the mean trait values for population 1 and 2, $s_p$ is the trait pooled standard deviation for the two populations, and $g$ is the number of generations the populations have been separated (Gingerich, 1993; Hendry & Kinnison, 1999). Within each temperature treatment, the Haldanes were calculated for the early life history traits with and without controlling for egg size effects to show how much egg size differences contribute to the observed divergence rates. We used least squares means to control for egg size effects. Any early life history traits not correlated with egg size or that had an egg size x population interaction in the linear mixed models were excluded.

## 2.3 Results

*Egg Size Comparison Among Populations*

The mean (mm ± SE) egg diameter of CR females (7.9 ± 0.10) was larger than both the PR (6.6 ± 0.09) and SR females (6.8 ± 0.09; $F_{2,65} = 51.18$, $P < 0.001$). The egg diameter of PR and SR females was no different. When female size was included as a

covariate, egg diameter was positively related to female size (Adj. $R^2 = 0.70$; $F_{1,63} = 21.80$, $P < 0.001$). After controlling for female size, the CR had a larger egg diameter than the PR, while the SR was no different than either population ($F_{2,63} = 12.20$, $P < 0.001$). The shift from an egg diameter difference between the CR and SR for the ANOVA to no difference for the ANCOVA indicates that the egg diameter difference between the populations is primarily driven by variation in female body size. In contrast, the difference in egg diameter between the CR and PR was maintained and was not explained by female body size.

*Egg Size and Multivariate Trait Comparisons*

Multivariate analysis revealed that the populations can be differentiated based on their early life history traits, with the strength of differentiation depending upon temperature regime (Figure 2.2, Table 2.1). The nMDS ordinations from each of the temperature treatments had stress values < 15 and were considered acceptable representations of the data (6.5°C = 0.06; 9.4°C = 0.11; 15.2°C = 0.04). The nMDS ordination plots show that the clearest separation occurs between the CR and the Lake Huron populations, particularly at the high temperature treatment (Figure 2.2). Differentiation between the PR and SR was generally weak, but most apparent at 15.2°C (Figure 2.2). The PERMANOVAs confirmed the patterns of separation (Table 1). The population effect in the PERMANOVA was strongest for comparisons between the CR and the Lake Huron populations ($R^2$ values; Table 2.1). For the PR and SR comparisons, the population effect was weak at the 6.5°C and 9.4 °C and increased at 15.2°C.

The trait distance matrices were positively correlated with the egg diameter distance matrices for all temperature treatments (Mantel test; 6.5°C: $r_M = 0.76$, $P = 0.001$; 9.4°C: $r_M = 0.70$, $P = 0.001$; 15.2°C: $r_M = 0.57$, $P = 0.001$). This positive correlation indicates that large family-wise differences in egg diameter are associated with large family-wise differences in early life history traits. The correlation between the trait and egg size distance matrices weakened with increasing temperature.

*Egg Size and Among Population Variation*

All the individual early life history traits were different among the populations before controlling for egg size (Table 2.2). Offspring from the CR tended to be larger and grow faster than those from the PR or SR, regardless of the temperature treatment. The main exception was the yolk sac conversion efficiency of the PR offspring, which was generally higher than that of the CR and SR. Egg diameter was positively related to most of the early life history traits; however, yolk sac conversion efficiency was negatively related to egg diameter and there was no relationship between egg diameter and swim-up to juvenile growth. When egg diameter was included in the analyses, the pattern of population differences depended on the temperature treatment (Table 2.2). In the 6.5°C treatment, there were slight changes in the population differences before and after controlling for egg size, but the CR and SR offspring generally performed better than the PR offspring. There were no clear patterns of population differences at 9.4°C (Table 2.2). Population differences at 15.2°C shifted after the hatching stage when controlling for egg size and the PR offspring started to out-perform the CR and SR offspring (Table 2.2). There were also several egg diameter x population interactions present, whereby the slopes of the egg diameter – trait relationships varied among populations (Table 2.2).

Egg diameter explained a large proportion of the variation in the early life history traits, which affected the variance explained by the population fixed effect and random effects in the linear mixed models (Figure 2.3). The strongest effect of egg size was on the population effect (i.e., among population variation), which showed a large decline in the variance explained between the models before and after egg size was included as a covariate (Figure 2.3a). However, the relative change in the variance explained by the population effect was most pronounced at 6.5°C (mean ± S.E.: 95% ± 1.3) and decreased with increased temperature (9.4°C: 85% ± 6.5; 15.2°C: 73% ± 11.0). The variance explained by the random effects also decreased when egg size was included in the models, but to a lesser extent than the population effect (Figure 2.3c). Unlike the population effect, temperature did not appear to significantly influence the relative change in the random effect variance (6.5°C: 50% ± 13; 9.4°C: 66% ± 14; 15.2°C: 30% ± 17). The variance explained by the full models did not change before and after egg

diameter was included in the models indicating that the variation explained by egg size was accounted for by the population fixed effect and random effects in the models without egg diameter.

*Egg size and Genetic Architecture*

The dam variance was significant for most traits before and after controlling for egg diameter and this was consistent across all temperature treatments, with the only exception being yolk sac volume at 15.2°C after controlling for egg diameter (Table 2.3). The addition of egg diameter into the models significantly reduced the dam variance components for all traits, regardless of temperature treatment (Table 2.3). The relative reduction of the dam variance components was consistently greater than 60% (Table 2.3). In contrast, the sire variance was significant for only a few of the traits before and after controlling for egg diameter in the models, and the sire variance components were minimally influenced by the inclusion of egg size as a covariate (Table 2.3). The only traits to show a significant change in the sire variance were hatch length and yolk sac volume at 9.4°C.

Maternal effects for the traits were influenced by the inclusion of egg diameter into the models, whereas the heritability was mostly unaffected. There was a significant reduction in the maternal effect for almost all traits at each temperature treatment when egg size was included into the models (non-overlapping confidence intervals; Figure 2.4). Hatch length at 15.2°C and yolk sac volume at 9.4°C were the only traits to show no change in the maternal effect. The heritability was generally unchanged before and after controlling for egg size, except for a decrease in the heritability of hatch length and yolk sac volume at 9.4°C and an increase in the heritability of swim-up length in 15.2°C (Figure 2.4).

The estimation of heritability and maternal effects was also influenced by temperature treatment. At 6.5°C, quantitative genetic analyses of hatch length, yolk sac volume, swim-up length, and juvenile length showed that these traits were primarily influenced by maternal effects, which were significantly larger than the heritability (non-overlapping confidence intervals for estimates from models without egg size; Figure 2.4).

Maternal effects were also greater than genetic effects for swim-up length and yolk sac conversion efficiency at 9.4°C and 15.2°C, respectively (Figure 2.4). At 9.4°C, the heritability was high and maternal effects were low for hatch length, yolk sac volume and juvenile length (Figure 2.4). At 15.2°C, maternal effects and heritability were no different for hatch length and swim-up length (Figure 2.4).

*Egg Size and Divergence Rates*

The estimated pair-wise divergence rates of the early life history traits were relatively high for divergence rates between the CR and the Lake Huron populations (PR and SR) before controlling for egg size, whereas the divergence rates were lower between the PR and SR (Figure 2.5). After controlling for egg diameter, there was a significant reduction in the estimated divergence rates at 6.5°C for the CR-PR and CR-SR comparisons, at 9.4°C for the CR-SR comparisons, and 15.2°C for the CR-PR comparisons (Figure 2.5). There were no significant differences between the PR-SR comparisons before and after controlling for egg size, regardless of temperature (Figure 2.5). The divergence rates for egg size were highest for the pair-wise comparisons between the CR and the Lake Huron populations (CR-PR = 0.28 and CR-SR = 0.24), whereas the divergence rate between the PR and SR was relatively low (0.06).

**Table 2.1** PERMANOVA results for the pairwise population comparisons of early life-history trait matrices at each temperature treatment. The PERMANOVAs were run for 999 iterations.

| Temperature | Pairwise Comparison | F-Statistic | $R^2$ | P-value |
|---|---|---|---|---|
| 6.5 °C | Credit – Pine | $F_{1,42} = 44.1$ | 0.51 | 0.001 |
| | Credit – Sydenham | $F_{1,40} = 20.3$ | 0.34 | 0.001 |
| | Pine – Sydenham | $F_{1,44} = 7.4$ | 0.14 | 0.002 |
| 9.4 °C | Credit – Pine | $F_{1,41} = 30.8$ | 0.43 | 0.001 |
| | Credit – Sydenham | $F_{1,37} = 23.9$ | 0.39 | 0.001 |
| | Pine – Sydenham | $F_{1,40} = 4.0$ | 0.09 | 0.01 |
| 15.2 °C | Credit – Pine | $F_{1,36} = 23.9$ | 0.40 | 0.001 |
| | Credit – Sydenham | $F_{1,34} = 19.7$ | 0.37 | 0.001 |
| | Pine – Sydenham | $F_{1,44} = 16.1$ | 0.27 | 0.001 |

**Table 2.2:** Comparisons of yolk sac volume ($mm^3$; YSV), hatch length (mm; HL), swim-up length (mm; SL), juvenile length (mm; JL), yolk sac conversion efficiency ($mm/mm^3$; YSCE), hatch to swim-up growth (mm/ΔD; HSGR), and swim-up to juvenile growth (mm/ΔD; SJGR) among progeny from the Credit River (C), Pine River (P), and Sydenham River (S) when reared under three different temperature treatments. The differences among the populations are presented as inequalities before (Base) and after (Egg) controlling for egg diameter variation in the analyses. If there was an egg diameter x population interaction, a comparison of slopes was provided (Pop. x Egg). The direction of the relationship between egg diameter and the traits is denoted with a superscript + or -. Only the population comparison is provided if there was no relationship between egg size and a trait.

| | | Base | Egg | |
|---|---|---|---|---|
| **Temp.** | **Trait** | **Pop.** | **Pop.** | **Pop. x Egg** |
| 6.5 °C | YSV | C > S > P | [C = S] > P $^{+}$ | |
| | HL | C > [S = P] | C = S = P $^{+}$ | |
| | SL | C > S > P | S > [C = P] $^{+}$ | |
| | JL | C > S > P | C = [S > P] $^{+}$ | |
| | YSCE | P > S > C | | [P > C] = S $^{-}$ |
| | HSGR | C > S > P | C = S = P $^{+}$ | |
| | SJGR | [C > P] = S | | |
| 9.4 °C | YSV | C > [S = P] | [C > P] = S $^{+}$ | |
| | HL | C > [S = P] | | P > [C = S] $^{+}$ |
| | SL | C > [S = P] | C = S = P $^{+}$ | |
| | JL | C > S > P | C = S = P $^{+}$ | |
| | YSCE | [P = S] > C | | [S = P] > C $^{-}$ |
| | HSGR | [C > S] = P | C = [P > S] $^{+}$ | |
| | SJGR | [C = S] > P | | |
| 15.2 °C | YSV | C > S > P | | C = [S > P] $^{+}$ |
| | HL | C > [S = P] | C = S = P $^{+}$ | |
| | SL | C > P > S | P > [C = S] $^{+}$ | |
| | YSCE | P > [C = S] | [C = P] > S $^{-}$ | |
| | HSGR | [C = P] > S | | P > [C = S] $^{+}$ |

**Table 2.3**: The estimated sire variance and dam variance for hatch length (HL), yolk sac volume (YSV), swim-up length (SL), and juvenile length (JL) at each temperature treatment. The variance components were estimated using a linear mixed model without egg diameter as a covariate (Before) and with egg diameter included as a covariate (After). Values in the brackets are the bias corrected and accelerated bootstrap 95% confidence intervals. Bolded variance estimates are those with a significant difference between the estimates before and after the inclusion of egg diameter as a covariate in the models (i.e. non-overlapping confidence intervals). The significance of the sire and dam variance components in the models was tested using a simulation-based restricted likelihood ratio test ($P < 0.05 = *$).

| | | **Sire Variance** | | **Dam Variance** | |
|---|---|---|---|---|---|
| **Trait** | **Temp.** | **Before** | **After** | **Before** | **After** |
| HL | 6.5 °C | 0.02 (0 - 0.05) | 0.01 (0.0 – 0.03) | **0.46 (0.42 - 0.51)*** | **0.11 (0.08 – 0.14)*** |
| | 9.4 °C | **0.13 (0.10 - 0.16)*** | **0.04 (0.03 – 0.06)*** | **0.28 (0.24 - 0.33)*** | **0.05 (0.03 – 0.07)*** |
| | 15.2 °C | 0.02 (0 - 0.07) | 0.004 (0.0 – 0.05) | **0.40 (0.33 - 0.47)*** | **0.21 (0.15 – 0.27)*** |
| YSV | 6.5 °C | 66.6 (0 - 167.4) | 0.0004 (0.0004 – 28.1) | **994.0 (873.0 - 1124.1)*** | **171.3 (99.8 – 243.6)*** |
| | 9.4 °C | **562.8 (485.3 – 644.5)*** | **142.9 (93.8 – 196.9)** | **542.9 (462.6 - 626.7)*** | **132.3 (68.9 – 196.1)*** |
| | 15.2 °C | 0.0003 (0.0 – 0.92) | 23.5 (0.0 – 62.8) | **446.2 (390.8 - 503.7)*** | **80.5 (33.7 – 129.5)** |
| SL | 6.5 °C | 0.08 (0.02 - 0.13) | 0.05 (0.02 – 0.09) | **1.08 (0.98 - 1.17)*** | **0.21 (0.17 – 0.24)*** |
| | 9.4 °C | 0.11 (0.07 - 0.15) | 0.05 (0.03 – 0.08) | **0.98 (0.89 - 1.07)*** | **0.22 (0.17 – 0.24)*** |
| | 15.2 °C | 0.19 (0.14 - 0.24) | 0.21 (0.16 – 0.26)* | **0.71 (0.62 - 0.79)*** | **0.22 (0.16 – 0.25)*** |
| JL | 6.5 °C | 0.20 (0.03 - 0.36) | 0.36 (0.22 – 0.50)* | **2.33 (2.01 - 2.52)*** | **0.82 (0.60 – 0.91)*** |
| | 9.4 °C | 0.70 (0.52 - 0.88)* | 0.67 (0.53 – 0.81)* | **2.01 (1.65 - 2.26)*** | **0.96 (0.63 – 1.23)*** |

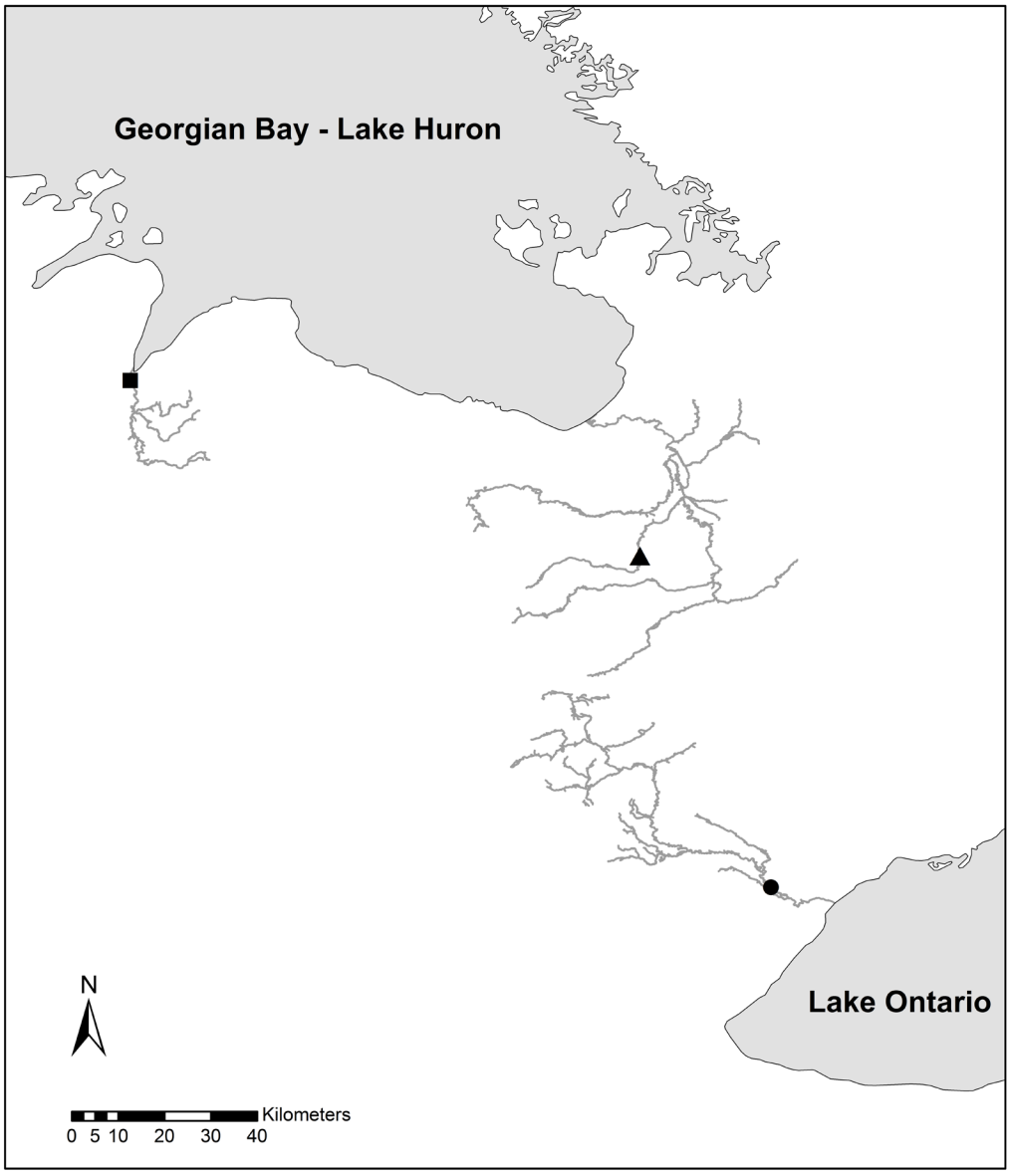


**Figure 2.1:** Location of the Credit River (circle), Pine River (triangle), and Sydenham River (square) Chinook salmon collection sites. All sites were located in Ontario, Canada. The map was created using publicly available data in ArcMap 10.3 (ESRI, 2015) and projected using UTM NAD83 zone 17N. River systems were simplified for display purposes.

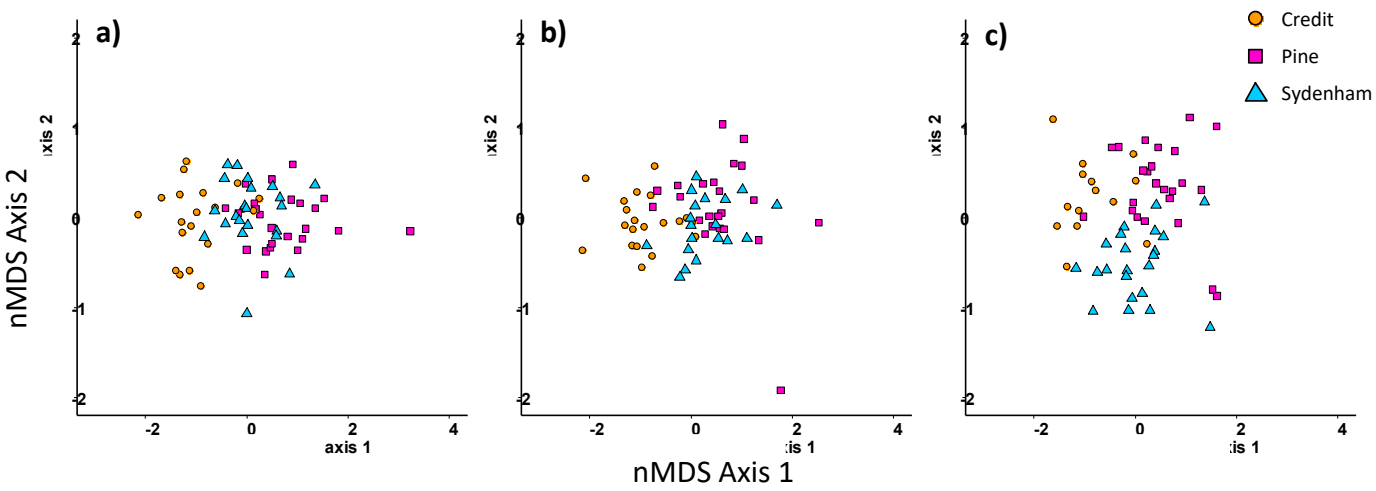


**Figure 2.2**: Non-metric multidimensional scaling (nMDS) ordination plots of early life-history traits from each population (Credit, Pine, and Sydenham Rivers) when reared in a hatchery under a) 6.5°C, b) 9.4°C, and c) 15.2°C. The trait matrices used for the ordination contained seven traits for the 6.5°C and 9.4°C temperature treatments and five traits for the 15.2°C temperature treatment.

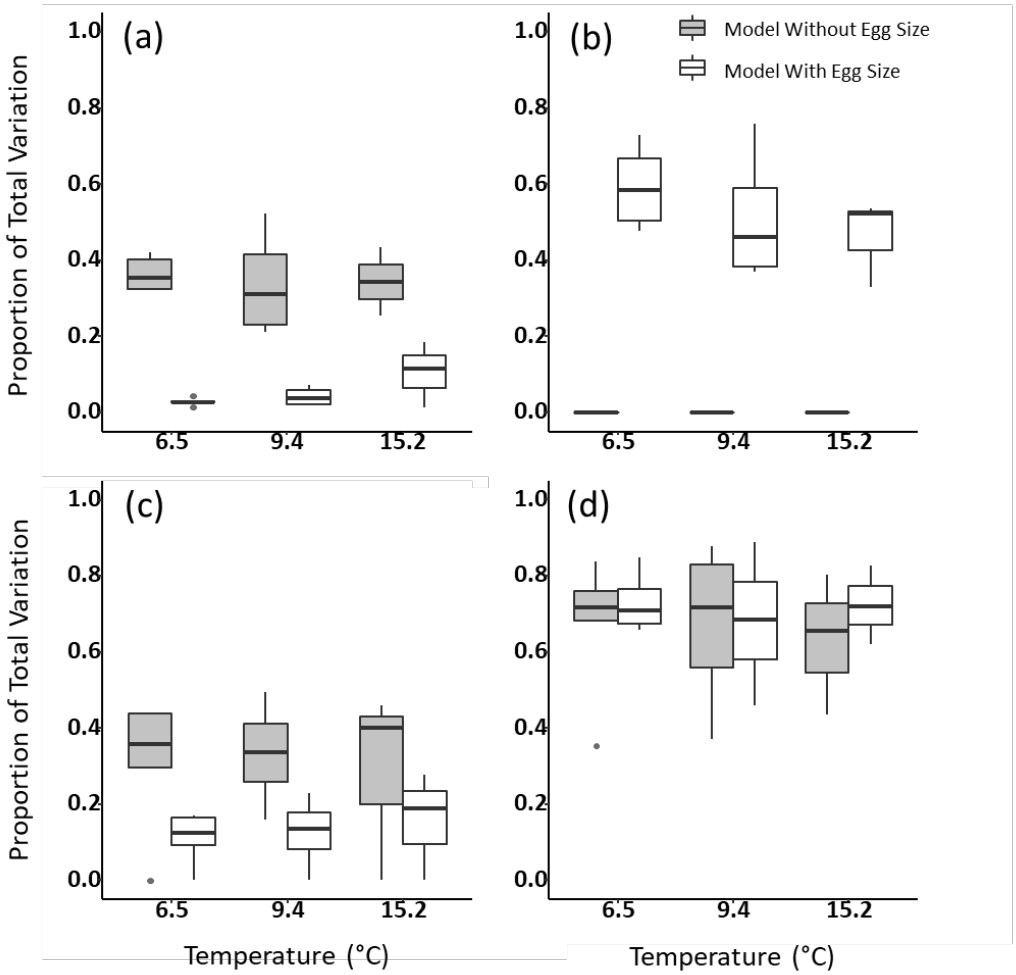


**Figure 2.3:** The proportion of variance explained by a) the population fixed effect, b) the egg size covariate, c) the random effects, and d) the fixed and random effects (i.e., full model) from linear mixed models comparing early life history traits among Chinook salmon populations at three temperatures. The linear mixed models were first fit with population as a fixed effect (grey) and then with population and egg size as fixed effects (white). Linear mixed models fit to length and volume data had sire and dam as random effects, whereas the growth traits had only sire as a random effect. Traits with a population x egg size interaction were excluded from this analysis because the individual effects of population and egg size could not be separated. The number of traits from 6.5°C, 9.4°C, and 15.2°C was 5, 4, and 3, respectively.

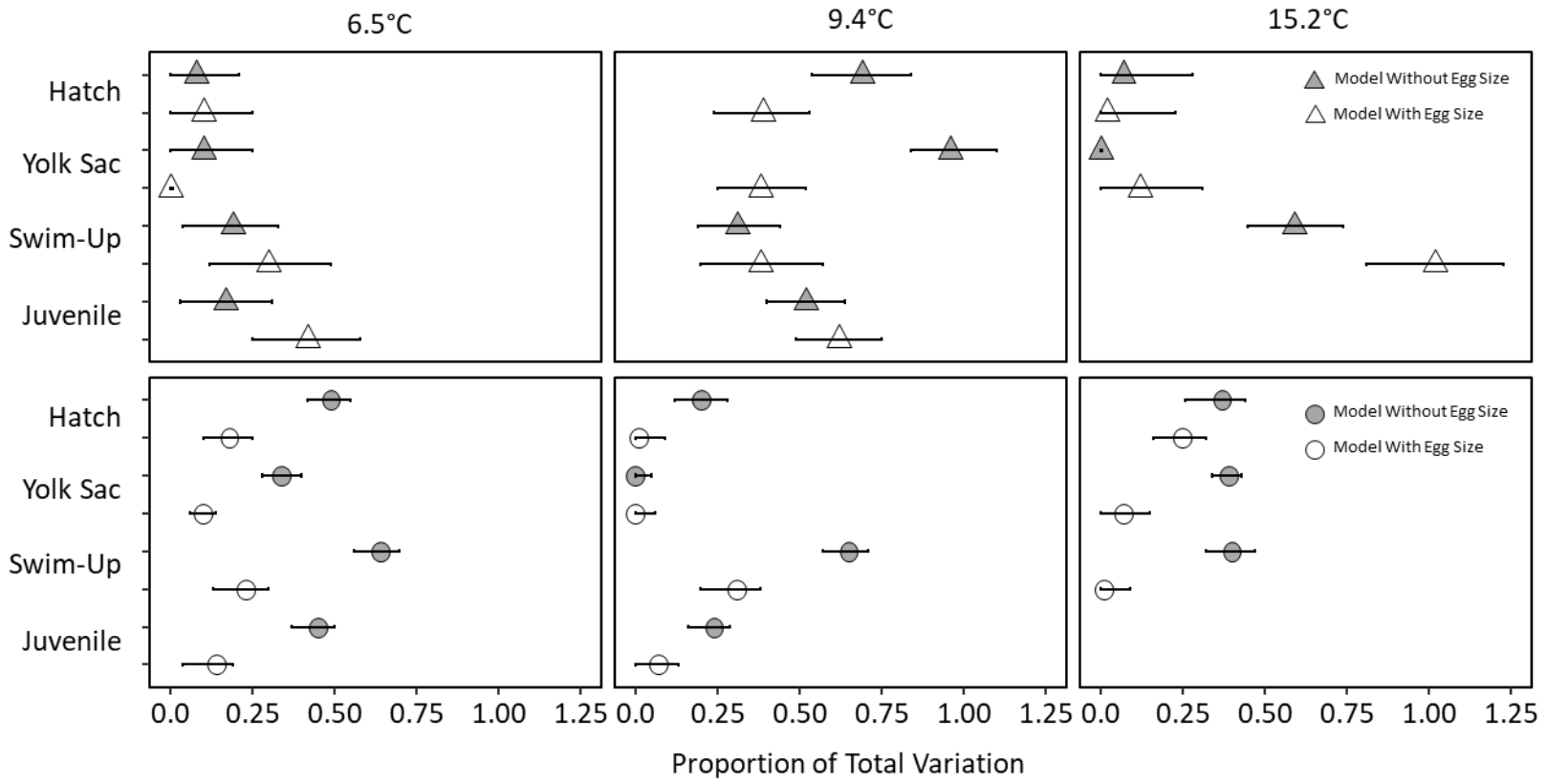


**Figure 2.4:** The heritability and maternal effect of hatch length, yolk sac volume, swim-up length, and juvenile length at each temperature treatment. The quantitative genetic parameters were estimated before (grey) and after (white) including egg size as a covariate in the linear mixed models. Error bars are the bias corrected and accelerated bootstrap 95% confidence intervals.

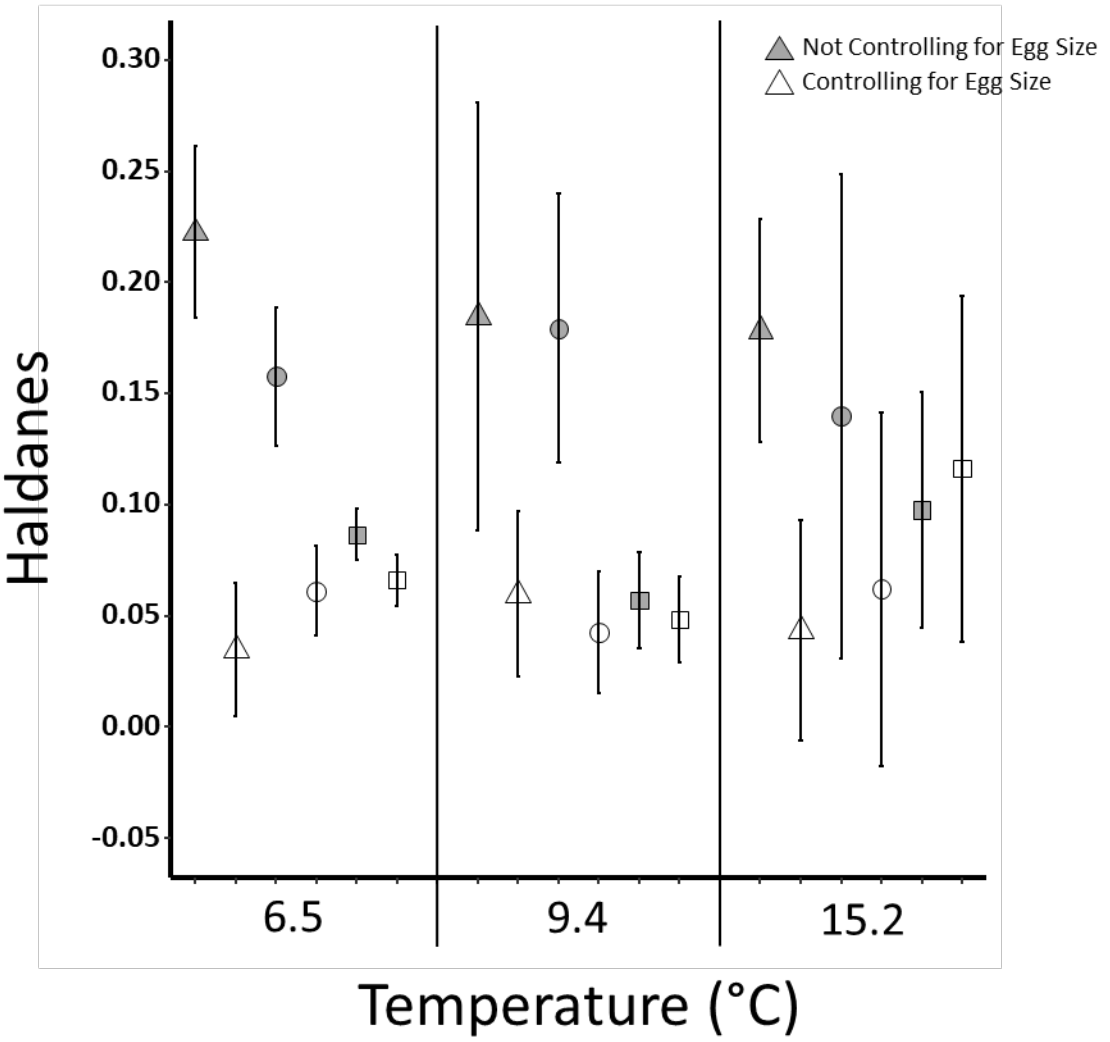


**Figure 2.5:** The mean (95% CI) divergence rate, in Haldanes, for the early life history traits before (grey) and after (white) controlling for egg size at each temperature. The divergence rates between the Credit-Pine (triangle), Credit-Sydenham (circle), and Sydenham-Pine (square) are presented separately. The mean and confidence intervals for the divergence rates were calculated using the estimated divergence rates of all traits within a temperature treatment for each pairwise population comparison. The number of traits used from 6.5°C, 9.4°C, and 15.2°C was 5, 4, and 3, respectively. The effect of egg size was controlled for using least squares means. Non-overlapping confidence intervals indicate a significant difference between the Haldanes before and after controlling for egg size.

## 2.4 Discussion

Using a common-garden hatchery study, I have shown that the early life history traits of introduced Great Lakes Chinook salmon populations have diverged within ~10 generations and that much of this divergence can be explained by variation in egg size. There was a strong relationship between egg size and most of the early life history traits, which resulted in egg size accounting for most of the among and within population variation. Interestingly, the among population variation explained by egg size decreased with an increase in temperature. Although egg size explained much of the variation in the traits, population differences remained after controlling for egg size suggesting that other effects, such as genetic, also contributed to the observed population differences. In general, my results are consistent with previous studies that have found evidence of population divergence among introduced salmonid populations on contemporary timescales (Haugen & Vøllestad, 2000; Hendry et al., 1998; Jensen et al., 2008; Kinnison et al., 1998; Koskinen et al., 2002; Thomassen, Barson, Haugen, & Vøllestad, 2011; Unwin, Quinn, Kinnison, & Boustead, 2000).

*Egg Size and Among Population Variation*

Egg size explained much of the among population variation in early life history traits across all the temperature treatments, which suggests that egg size variation is the primary driver of trait divergence among populations. Previous studies of introduced salmonids have mostly been interested in identifying the genetic effects underlying phenotypic divergence among populations (Hendry et al., 1998; Jensen et al., 2008; Kinnison et al., 1998; Koskinen et al., 2002; Thomassen et al., 2011; Unwin et al., 2000). However, my results suggest that any genetic effects contributing to the phenotypic divergence of early life history traits are minimal and that egg size can explain up to 100% of the among population variation. This has significant implications for the contemporary evolution of early life history traits because it suggests that egg size has a much greater capacity to alter offspring phenotypes in response to environmental changes than genetic effects on ecological timescales.

Phenotypic divergence rates are often used to quantify the among population variation in a phenotype per unit time (reviewed Hendry & Kinnison, 1999; Kinnison & Hendry, 2001). Prior to controlling for egg size, the phenotypic divergence rates of the early life history traits were similar to other studies of introduced salmonids, which have found divergence rates ranging from 0.007 − 0.36 (Haugen & Vøllestad, 2001; Hendry & Kinnison, 1999). These phenotypic divergence rates incorporate all components of a phenotype, such as genetic, maternal, and environmental effects (Hendry & Kinnison, 1999). Researchers often attempt to estimate the genetic divergence rates of traits (i.e., divergence attributable only to genetic effects; Reznick, Shaw, Rodd, & Shaw, 1997); however, few studies have attempted to assess the maternal contribution to divergence rates. Badyaev (2005) showed that degree of divergence among juvenile house finch (*Carpodacus mexicanus*) traits was positively related to the proportion of maternal variation underlying the traits. Similarly, we found that controlling for egg size reduced the mean divergence rate of the early life history traits for several of the pair-wise population comparisons indicating that egg size makes a significant contribution to population divergence.

*Egg Size and Genetic Architecture*

Egg size was a strong maternal effect trait and significantly reduced both the dam variance and maternal effect for most of the early life history traits. Both the univariate and multivariate analyses revealed that there is strong relationship between the early life history traits and egg size across all temperature regimes. This strong relationship is consistent with previous studies on salmonids (Beacham & Murray, 1985, 1990; Einum & Fleming, 2004; Haugen & Vøllestad, 2000; Hendry et al., 1998) and reflects the dependence of offspring development on the maternal per-offspring allocation of resources (i.e., egg size and energy; Einum, Kinnison, & Hendry, 2004; Rollinson & Rowe, 2016). Though egg size explained most of the dam variance and maternal effect in our study, there are other potential sources of maternal variation, such as hormones, nutrients, immune factors, and mRNA (Brooks, Tyler, & Sumpter, 1997). Future studies can incorporate these additional maternal effect traits into models to better understand their relative importance to the expression of phenotypic variation in early life.

Maternal effects were generally stronger than additive genetic effects for the early life history traits, which has often been found by other quantitative genetic studies of salmonids (Falica et al., 2017; Heath et al., 1999; Houde et al., 2013; Kinnison et al., 1998; Páez et al., 2010; Pitcher & Neff, 2007). Because genetic effects are often weak during early life, one might conclude that early life history traits will have a limited capacity to adapt to new or changing environments (e.g., climate change), but this is at odds with the growing body of evidence from studies of contemporary evolution in salmonids (e.g., Haugen & Vøllestad, 2000; Hendry et al., 1998; Kinnison et al., 1998). The disconnect lies in the assumption that egg size variation, the primary maternal effect trait, is purely an environmental effect. Egg size is a heritable trait (Carlson & Seamons, 2008; Heath, Heath, Bryden, Johnson, & Fox, 2003; Kinnison, Unwin, Hendry, & Quinn, 2001) and the genes controlling egg size represent an indirect genetic effect that can influence the evolution of early life history traits (McAdam et al., 2014; Wolf, Brodie III, Cheverud, Moore, & Wade, 1998). Therefore, changes in egg size could be an important pathway through which early life history traits could evolve in salmon even when the additive genetic effects are weak.

As the offspring progressed through ontogeny, there was no consistent reduction in the maternal effect with age. Previous studies have found that the maternal effect decreases as development progresses because offspring become more self-reliant and additive genetic effects become more apparent (Heath et al., 1999; Wilson, Kruuk, & Coltman, 2005). Our experiment was terminated mid-way through the juvenile free-feeding stage, and likely did not provide enough time for the influence of maternal effects to disappear as in other longer term studies. Selection during the early life history stage is often size-dependent (reviewed by Sogard, 1997), and the strong influence that maternal effects have on size-related early life history traits indicates that aspects of the maternal environment, such as egg size, have important fitness consequences during this early developmental stage.

*Egg Size Effect and Temperature*

The strength of the egg size effect on the among population variation in early life history traits decreased with an increase in rearing temperature. This suggests that the importance of egg size for mediating adaptation, in the context of introductions or climate change, might be lessened at elevated stream temperatures. Such a temperature dependent association was supported by the reduced effect of egg size on the among population variation at warm temperatures as well as the consistent decrease in the correlation between trait and egg size distance matrices with increased temperature. The temperature dependence of the egg size effect may be related to changes in the body size – metabolic rate relationship. Chinook salmon are adapted to cold-water environments and temperatures above ~12°C are considered to be stressful during early life, which is well below the highest temperature treatment used in our study (reviewed by Richter & Kolmes, 2005). Régnier et al. (2013) studied the relationship between metabolic rate and body size for brown trout (*Salmo trutta*) alevins across three temperature treatments and found that metabolic rate was highly variable and no longer scaled with body size at high temperature (14.5°C). Since the body size of salmon progeny is positively related to egg size, a breakdown in the body size – metabolic rate relationship at high temperature would also impact the body size – egg size relationship and result in a reduced egg size effect on growth related early life history traits at high temperature. The standard error of hatch to swim-up growth rate for salmon in our study did increase in the 15.2°C treatment for two populations lending some support to the idea that changes in metabolic rate contributed to the weakened egg size effects at high temperature (Appendix A.3).

An increase in the expression of additive genetic effects with temperature could be another explanation for the reduced effect of egg size on the among population variation at warm temperatures (Charmantier & Garant, 2005; Hoffmann & Merilä, 1999). Rearing in a stressful or novel environment can lead to the release of "cryptic" genetic variation, which increases the expression of additive genetic variance and reduces the maternal and/or environmental variance of a trait (Hayden, Ferrada, & Wagner, 2011; Lynch & Walsh, 1998; McGuigan, Nishimura, Currey, Hurwit, & Cresko, 2011; Purchase & Moreau, 2012; Rutherford, 2000). However, there was no consistent increase

in the additive genetic variance or heritability of traits in the warm treatment relative to the colder treatments, which makes cryptic genetic variation an unlikely explanation for the reduced effect of egg size on the among population variation at warm temperatures.

Interestingly, the heritability was greater than maternal effects for hatch length, yolk sac volume, and juvenile length in the medium treatment, but not at any other temperature treatment (i.e., genotype x environment interaction). The change in the heritability with temperature was primarily due to an increase in the additive genetic variance at 9.4°C, and not due to a consistent change in the dam or environmental variance (Appendix A.4). The increase in the heritability of the traits in the medium treatment is consistent with the results of a meta-analysis by Charmantier and Garant (2005) who found that heritability was greater in "favourable" environmental conditions. We consider our medium treatment as the most favourable thermal condition because it is closest to the optimal growth temperature for Chinook salmon during their early life history stage (Richter & Kolmes, 2005). In contrast, the warm treatment may have been stressful enough to constrain the expression of additive genetic variation leading to the low additive genetic variance we observed for traits in that treatment. An implication of this finding is that the presence of environmental heterogeneity in the wild, such as differences in environmental conditions among salmon redds, could lead to spatial/temporal variation of genetic effects within a population making it difficult to predict the response of a population to selection (Charmantier & Garant, 2005). The change in the additive genetic variance with temperature also highlights the need for studies to rear populations under a range of possible environmental conditions likely to be experienced in the wild (if the wild is not logistically feasible) in order to more rigorously assess whether the evolution of phenotypic traits is constrained by a lack of additive genetic variation.

*Egg Size Differences Among Populations*

Variation in egg size among the Great Lakes Chinook salmon populations could be related to differences in maternal size and/or egg size selection regimes. There is a well known positive relationship between maternal size and egg size in salmonids (Einum

et al., 2004) and the difference in egg size between the CR and SR was primarily explained by variation in maternal size-at-maturity. These differences in size at maturity are likely due to differences in growth opportunities within their respective lake environments because the SR and CR have a similar age-at-maturity (Haring et al., 2016; Suk et al., 2012). In contrast, maternal size could not explain the differences in egg size between the CR and PR. These populations continued to have an egg size difference even after controlling for female size, which might indicate that egg size is being differentially selected for in these populations. Egg size can be influenced by pre- and post-zygotic selection pressures, such as variation in the temperature experienced by the mother during egg maturation (Jonsson & Jonsson, 2016), the natal stream temperature (Braun, Patterson, & Reynolds, 2013), the length of upstream migration (Kinnison et al., 2001), and the incubation gravel size (Quinn, Hendry, & Wetzel, 1995). Kinnison et al. (2001) found that salmon populations with a longer upstream migration produced smaller eggs than those with a shorter migration. The PR population has a much longer migration distance (> 100 km) than the CR (~14 km) and, consistent with Kinnison et al. (2001), the PR produced smaller eggs. Further research is needed to disentangle the various environmental factors contributing to the egg size differences among the populations.

## 2.5 Conclusion

I provide evidence that the early life history traits of Great Lakes Chinook salmon populations have diverged within ~10 generations and that egg size explained most of the observed among population variation. However, the contribution of egg size to the among population variation decreased with an increase in temperature indicating that other effects contribute at high temperature. Within populations, the dam variance and maternal effect were generally the most influential source of phenotypic variation, regardless of temperature. Egg size explained much of the maternal effect suggesting that egg size is the primary maternal effect trait influencing offspring phenotypes. Overall, egg size appeared to mediate the primary response of early life history phenotypes when introduced into a new environment, while genetic effects provided a limited amount of additional phenotypic variation. These results highlight the integral role egg size plays in the contemporary evolution of fish early life history traits and future studies are needed to

better understand the genetic and environmental effects shaping egg size and offspring traits. Such studies will be required if we are to reliably predict the response of early life history traits to environmental change.

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# 3 Transgenerational effects of egg nutrients on the early development of Chinook salmon (*Oncorhynchus tshawytscha*) across a thermal gradient[2]

## 3.1 Introduction

Transgenerational effects arise when the parental phenotype or environment shapes the development and phenotypic traits of offspring (i.e., parental effects; Badyaev & Uller, 2009). These transgenerational effects can be transferred to the offspring generation through epigenetic variation, milk or yolk resources, hormones, immune factors, or behaviours (Bonduriansky, Crean, & Day, 2012). They can have profound fitness consequences for offspring and have been found to occur in a wide variety of taxa (Coslovsky & Richner, 2011; Franzke & Reinhold, 2013; Galloway & Etterson, 2007; Hafer, Ebil, Uller, & Pike, 2011; Helle, Koskela, & Mappes, 2012; Salinas & Munch, 2012; Shama et al., 2016; Shama, Strobel, Mark, & Wegner, 2014; Storm & Lima, 2010; Triggs & Knell, 2012; Zizzari, van Straalen, & Ellers, 2016). Although there is evidence of paternal effects (Etterson & Galloway, 2002; Triggs & Knell, 2012), most transgenerational effects are mediated by maternal effects because mothers tend to control the allocation of resources to offspring (Bernardo, 1996; Mousseau & Fox, 1998; Räsänen & Kruuk, 2007). In most fish species, mothers provide little parental care and the manipulation of egg quality is an important mechanism through which environmental cues are transmitted to offspring (Jonsson & Jonsson, 2016; Segers & Taborsky, 2012).

The quality of an egg is typically characterized in terms of egg size and the quality of nutrient stores (Brooks et al., 1997; Kjorsvik, Mangor-Jensen, & Holmefjord, 1990). Much of the research on egg quality has focused on egg size because of its close association with offspring size and fitness (Einum & Fleming, 1999, 2000; Heath & Blouw, 1998). Because there is a consistent, positive relationship between egg size and

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[2] Thorn, M.W., Dick, M.F., Oviedo, L., Guglielmo, C.G., & Morbey, Y.E. (in press). Transgenerational effects of egg nutrients on the early development of Chinook salmon (*Oncorhynchus tshawytscha*) across a thermal gradient. Canadian Journal of Fisheries and Aquatic Sciences. doi: 10.1139/cjfas-2018-0013.

offspring size, the effects of egg size variation on offspring phenotypes is well understood (Heath & Blouw, 1998). In contrast, the influence of egg nutrient composition on offspring traits is not as clear.

Yolk nutrients are deposited in the egg during vitellogenesis in the months or weeks prior to spawning (Johnson, 2009; Lubzens, Young, Bobe, & Cerdà, 2010; Tyler & Sumpter, 1996; Wiegand, 1996). Yolk nutrients are broadly composed of lipids, protein, carbohydrate, and micronutrients (Brooks et al., 1997). Of these components, lipids are the primary energy resource used by fish during the endogenous feeding stage (Wiegand, 1996). Lipids also serve as precursors for hormones, and have important structural and functional roles in cell membranes (Sargent, Bell, McEvoy, Tocher, & Estevez, 1999; Wiegand, 1996). The diverse functions of lipids during development are supported by the various fatty acids (FAs) that form the lipid reserve. Essential polyunsaturated fatty acids (PUFAs) from the n-3 and n-6 series are particularly important because they cannot be synthesized de novo, and are required for the proper development and survival of offspring (Sargent et al., 1999). Docosahexaenoic acid (DHA, 22:6n-3) is found in high concentrations in the retina, brain, and spinal cord of fishes (Bell & Dick, 1991; Mourente, 2003) and deficiencies in DHA have been associated with impaired visual systems, brain development, and larval behaviour (Bell et al., 1995; Ishizaki et al., 2001). DHA and eicosapentaenoic acid (EPA, 20:5n-3) are major polyunsaturated FAs found in the cell membranes of fishes and support cell membrane function and integrity (Sargent et al., 1999; Sargent, Bell, Bell, Henderson, & Tocher, 1995). The DHA/EPA ratio has been shown to affect offspring development because of the competitive interactions between these fatty acids in metabolism (Gapasin & Duray, 2001; Rodriguez et al., 1997; Watanabe, 1993). Furthermore, EPA and arachidonic acid (ARA, 20:4n-6) both serve as precursors to eicosanoid hormones that are essential for the regulation of various physiological processes (Sargent et al., 1995; Tocher, 2003). Overall, offspring that have lipid stores low in DHA, EPA, and ARA experience reduced growth, neural development, and survival (Copeman, Parrish, Brown, & Harel, 2002; Sargent et al., 1995; Wiegand, 1996).

The thermal environment that offspring experience can influence how the fatty acid composition and quantity of lipid affect development and survival. Because fish are poikilothermic, most physiological processes are affected by water temperature. The membrane function of a cell is affected by temperature (e.g., membrane fluidity) and the maintenance of membrane function at different temperatures requires membrane lipids with qualities that match the environment (March, 1993; Robertson & Hazel, 1997). For example, there is a general shift in the lipid composition of cell membranes from unsaturated FAs, mostly PUFA, at low temperatures to more saturated FAs at warm temperatures (Hazel, 1984, 1995; Robertson & Hazel, 1997). This shift in FAs with temperature is apparent at the individual level with larval fishes having a greater ratio of polyunsaturated to saturated fatty acids (PUFA:SFA) when raised at low temperatures relative those raised at higher temperatures (Laurel, Copeman, & Parrish, 2012). Furthermore, the ability of fish to digest SFAs decreases with a decrease in temperature, whereas the digestibility of PUFAs is not appreciably influenced by temperature (Ng, Sigholt, & Gordon Bell, 2004). Finally, an increase in temperature can lead to a higher metabolic rate (Clarke & Johnson, 1999) and cost of development (Mueller et al., 2015) as well as a reduced yolk sac conversion efficiency (Heming, 1982; Rombough, 1994), which means that a developing embryo/larva can have a higher energy demand in warm water and require greater lipid stores for growth.

Most of our knowledge about the effects of FA composition on offspring development is derived from aquaculture studies using simplified or enriched diets that do not accurately reflect the complex natural diets of fishes. In the wild, lipids deposited in the egg are either derived directly from the maternal diet or from stored lipids in somatic and visceral tissues (i.e., indirectly from diet; Johnson, 2009; Wiegand, 1996). FAs that are $\geq 14$ carbons long are often stored with little to no modification into the tissues of vertebrates (Iverson, 2009). As a result, the composition of the FAs in the tissues of fishes largely reflects their diet, albeit integrated over different timescales depending on the tissue (Budge, Iverson, & Koopman, 2006; Iverson, 2009). This quality of FAs has been used to infer dietary differences among populations or ecotypes (i.e., trophic biomarker; Ashton, Farkvam, & March, 1993; Scharnweber, Strandberg, Marklund, & Eklöv, 2016; Torniainen et al., 2017; Wiegand et al., 2007; Wiegand,

Johnston, Martin, & Leggett, 2004), and to determine food web structure (Happel et al., 2016; Mohan, Connelly, Harris, Dunton, & McClelland, 2016; Strandberg et al., 2015). Previous studies have shown that the FA composition of eggs can vary among populations when exposed to different diets (Ashton et al., 1993; Wiegand et al., 2004) and that this variation can influence offspring phenotypes by shaping the quantity of essential FAs and energy available for development (Czesny, Dettmers, Rinchard, & Dabrowski, 2009). However, there is a lack of research on how natural variation in FA composition can influence offspring growth and survival across an environmental gradient.

Here, I use Laurentian Great Lakes Chinook salmon (*Oncorhynchus tshawytscha*) populations to test the hypothesis that variation in egg FA and proximate composition will affect the expression of offspring phenotypes during the endogenous feeding stage at different temperatures. I predict that offspring growth and survival will be positively related to the relative quantity of PUFAs in eggs at low temperature, and that this relationship will decrease in strength with an increase in temperature. I also predict that offspring growth and survival will be positively related to the relative quantity of lipids in eggs, and that this relationship will increase with an increase in temperature. I also tested the hypothesis that the FA composition of eggs can serve as a trophic biomarker and will be different among Chinook salmon populations. Chinook salmon forage in the Great Lakes proper until they reach sexual maturity. While foraging, Chinook salmon originating from different regions within a lake are heterogeneously distributed both spatially and temporally (Marklevitz, Fryer, Johnson, Gonder, & Morbey, 2016). Chinook salmon also show philopatry to their natal spawning tributaries and populations will stage at the mouth of their natal tributaries until there are favourable environmental conditions for upstream migration (Adlerstein, Rutherford, Clapp, Clevenger, & Johnson, 2007). These spatially variable foraging patterns may expose Chinook salmon populations to different prey communities throughout oogenesis resulting in population differences in the FA composition of eggs.

## 3.2 Materials and Methods

*Gamete Collection*

Eggs and sperm were collected from sexually mature, pre-spawning Chinook salmon captured in the Credit (43°34'39.58"N, 79°42'8.57"W), Pine (44°13'10.12"N, 79°57'24.84"W), and Sydenham (44°33'34.36"N, 80°56'39.49"W) Rivers. Chinook salmon were captured in the Credit River on 1 October 2012 using electrofishing, in the Pine River from 19-27 September 2012 using a combination of dip nets and seine nets, and in the Sydenham River from 22 September – 06 October 2012 using a fish trap built into the Mill Street Dam. Water temperatures at the time of capture were 14°C, 10-12°C, and 12.5-14.5°C for the Credit, Pine, and Sydenham Rivers, respectively. All captured individuals were first assessed for sexual maturity by massaging the abdomen to determine if eggs/sperm were readily released. Those found to be sexually mature (i.e., released gametes) were anesthetized by immersing them in a clove oil solution (20 $mg \cdot L^{-1}$), measured for fork length, and a sample of eggs (~500) or milt (few millilitres) was collected. Visually unhealthy salmon (e.g., emaciated, skin lesions or tumors) were not used for this experiment and I released all Chinook salmon after sampling was complete. The collected eggs and milt were stored in a cooler at ~ 4°C and transported directly back to the hatchery at Western University. Once at the hatchery, half the eggs from each female were used for hatchery rearing, thirty were placed in cryotubes and put in a freezer at -80°C for fatty acid analysis, and the remainder were put in a freezer at -20°C for proximate composition analysis.

*Egg Mass and Proximate Composition*

A total of 18 Credit River, 26 Pine River, and 21 Sydenham River females were used for egg mass and composition analysis. Twenty-five eggs per female were weighed to determine egg wet mass. The proximate composition of the eggs from each female was determined by measuring the fat, lean mass, and water content. Several eggs from each female (~10) were dried at 60°C for ~ 48 hours until a stable dry mass was obtained. The dried samples were then crushed into a fine powder using a mortar and pestle. The fat was extracted from the samples using a Soxhlet apparatus and petroleum ether (30-60°C

BP) for 8 hours. Petroleum ether was used to extract fat from the dried egg samples because it extracts neutral lipids, which are used as energy reserves, and not structural lipids (Dobush, Ankney, & Krementz, 1985). The lean mass left over after fat extraction is composed of protein, ash, and carbohydrate. Previous studies on salmon have shown that the lean mass of salmon tissues is primarily composed of protein (~97%), while ash (~2 %) and carbohydrate (< 0.5%) are found in small quantities (Hendry & Berg, 1999; Jonsson & Jonsson, 1997; Jonsson, Jonsson, & Hansen, 1997). The proximate composition of eggs was calculated as the percent fat, lean mass, and water of egg wet mass, and as the percent fat and lean mass of egg dry mass.

*Egg Fatty Acid Profiles*

Egg fatty acid composition was determined by first extracting the total lipids from a sample of 6-10 eggs per female using the Folch, Lees, & Stanley (1957) method. Each sample of eggs was homogenized and ~ 50 mg was transferred to a centrifuge tube containing 2 mL of chloroform:methanol (2:1 v/v) with 0.01% butylated hydroxytoluene (BHT). Heptadecanoic acid (17:0, 3 mg/ml) was then added to the solution as an internal standard and the solution was centrifuged at 3000 rpm for 15 minutes. After centrifugation, 1 mL of 0.25% potassium chloride was added to the solution and the centrifuge tube was placed in a warm water bath at 70°C for 10 minutes. The aqueous layer was then discarded and the remaining organic layer was transferred to a pre-weighed 4 mL vial. The sample was dried using a gentle stream of nitrogen, reweighed to determine total lipid, and then redissolved using a solution of choloform:methanol (2:1 v/v) with 0.01% BHT to a concentration of 1-5 mg sample$\cdot$mL$^{-1}$ solution.

I then transferred 150 µg of the total lipid sample to a 2 mL vial and dried under nitrogen. 0.5 N Methanolic-HCl (200 µg) was then added to the dried sample and placed in a drying oven at 90°C for 30 minutes to covert the fatty acids to methyl esters. Then 800 µL of ultrapure water was added after cooling, and three successive extractions were done on the sample using 500 µL of hexane. The hexane extractions were combined, dried under nitrogen, and redissolved using 100 µL hexane. The fatty acid methyl esters were separated using an Agilent 6890N gas chromatograph (Agilent Technologies, Santa

Clara, CA, USA). We used a DB-23 high resolution column (Agilent Technologies), a flame ionization detector, and helium as a carrier gas (1.9 ml·minute$^{-1}$). The temperature program was 2 minutes at 80°C, temperature increase to 180°C at a rate of 5°C per minute, hold for 3 minutes, increase to 200°C at a rate of 1.5°C per minute, hold for 0 minutes, increase the temperature to 240°C at a rate of 10°C per minute, and hold for 3 minutes at 240°C. The fatty acids were identified by comparing the relative retention times (retention time/retention time of internal standard) to those derived from known standards (Supelco 37 FAME Mix, Supelco C8-C24 FAME Mix, and Supelco PUFA no. 3 from menhaden oil, Sigma-Aldrich). For our analyses, we did not include fatty acids with a composition < 0.1% of the total lipid content. This resulted in the removal of 20:0, 22:0, 24:0, 22:1(n-9), 24:1(n-9), 16:3(n-4), 22:2(n-6), and 22:5(n-6) from the dataset.

*Hatchery Rearing*

Eggs from each female were partitioned into six egg containers (40 eggs per container; 6 cm diameter x 5 cm height) and then fertilized with milt from males of the same population using a paternal half-sibling breeding design (1 male x 2 females; Lynch & Walsh, 1998). A paternal half-sib breeding design was used because it allowed us to fertilize the greatest number of unique females, while also controlling for genetic effects, relative to other breeding designs, such as maternal half-sib or family block designs. The fertilizations resulted in 18 Credit River, 26 Pine River, and 21 Sydenham River families. Two egg containers per family (80 eggs) were then transferred to upwelling incubation trays at a mean temperature (°C ± S.D.) of 6.5 ± 0.8, 9.4 ± 0.3, and 15.2 ± 0.02. These temperature regimes reflect the natural range of temperatures the populations would experience in the wild during incubation (range: 18°C - 0°C; Thorn & Morbey, 2018). Dead/unfertilized eggs (i.e., white in colour) were removed from egg containers daily. All removed eggs were preserved in Stockard's solution and later assessed for evidence of embryonic development (Boyd et al., 2010). This allowed for the calculation of hatch success (i.e., the number of live alevins) by excluding unfertilized embryos. The developing embryos remained in the egg containers until the study was terminated at swim-up stage, which is when the fish have fully absorbed the yolk sac. Swim-up was chosen as the end point of the experiment because swim-up is the last point at which the

offspring are still dependent on maternally derived energy stores. All animal procedures were approved by the Western University Animal Care Subcommittee (2007-043-05).

*Early Life History Traits*

I measured hatch length, swim-up length, hatch to swim-up growth rate, hatch success, and hatch to swim-up survival during the experiment. All length measurements were taken from the anterior tip of the snout to the posterior tip of the hypural plate (i.e., standard length). The hatch length of individuals from each family was measured by taking a photograph of a family in a petri dish of water at 50% hatch and using the computer software ImageJ (https://imagej.nih.gov/ij/) to measure the individuals in the photograph. The position of the petri dish was constant among photographs and a ruler was placed in each picture for scale. Swim-up length was measured using a set of hand held calipers to the nearest 0.1 mm. ImageJ was used to measure hatch length instead of calipers to reduce handling stress and any associated mortalities. I validated the use of ImageJ by measuring a subset of individuals using both calipers and ImageJ, and found that the two techniques produced highly consistent measurements (linear regression: $\beta = 0.99 \pm$ S.E. 0.04, $P < 0.001$, $R^2 = 0.98$, $N = 15$). Hatch to swim-up growth rate was calculated as:

$$G = \frac{L_S - L_H}{\Delta D}$$

where $L_S$ is swim-up length (mm), $L_H$ is hatch length (mm), and $\Delta D$ is the number of degree days between hatch and swim-up length measurements (Jensen et al., 2008). Degree days were calculated as the sum of mean daily water temperatures over the period of time between hatch and swim-up (Jensen et al., 2008). Hatch success was measured as the number of fertilized embryos that successfully hatched. Finally, hatch to swim-up survival was the number of live alevins that survived until the termination of the experiment at the swim-up stage. All sample sizes and summary data for the early life history traits by population and temperature can be found in Appendix B.1 and B.2.

*Statistical Analysis*

Statistical analyses were conducted using family means for length and growth traits, and individual data for survival traits in the R statistical computing environment (R Core Team, 2016). Egg wet mass and proximate composition were compared among the populations using an analysis of variance (ANOVA) and post-hoc Tukey tests. Given that egg mass is often correlated with female length, I also compared egg mass among the populations using an ANCOVA with female length as a covariate. The egg fatty acid composition was compared among the populations using principal components analysis (PCA; Tabachnick & Fidell, 2007). The fatty acid composition data was first arcsine square root transformed to normalize the data. Principal component scores with eigenvalues > 1 were compared among populations using an ANOVA to determine if there were any significant differences in egg fatty acid composition among populations (Tabachnick & Fidell, 2007).

Linear and generalized linear mixed models were used to assess the effects of egg fatty acid composition on growth/size and survival traits, respectively. We first fit a "full" model using the general form:

$$Z = \mu + P + T + EG + PC_n + L + P\,x\,T + P\,x\,E + T\,x\,E + P\,x\,PC_n + T\,x\,PC_n + P\,x\,L + T\,x\,L + Sire + e$$

where $P$ is the population of origin, $T$ is the temperature treatment, $E$ is the mean egg mass of each family, $PC_n$ is the n$^{th}$ principal component from the PCA, $L$ is the proportion of egg dry mass that was lipid, $Sire$ is the random effect of sire, and $e$ is the unexplained residual variation. The generalized linear models contained the additional random effect of female identity nested in sire. All possible two-way interactions with temperature and population were included in the model. Linear and generalized linear mixed models were fit using the lme4 package (Bates et al., 2015). I then performed backwards stepwise model selection by iteratively removing non-significant terms from the model until the log-likelihood of the nested model was significantly reduced ($\alpha = 0.05$; Appendix B.3; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). I first removed non-significant two-way interactions and then removed non-significant main effects. The variables retained in the reduced models were individually assessed by removing each variable from the model

and comparing the nested model with the full model using a likelihood ratio test. The variance explained by the fixed effects (marginal $R^2$) and the full model (conditional $R^2$) was calculated for the final models following Nakagawa & Schielzeth (2013). I visualized interactions between temperature/population and the egg composition metrics using partial dependence plots. Relationships were plotted with 95% confidence intervals estimated using parametric bootstrapping run for 500 iterations.

## 3.3 Results

*Egg Wet Mass and Proximate Composition*

Egg wet mass was different among the three populations with the Credit River having the heaviest eggs and the Pine River having the lightest eggs ($F_{2,62} = 41.2$, $P < 0.001$; Table 3.1). After controlling for female length, egg wet mass was similar between the Credit and Sydenham Rivers, while the Pine River had significantly lighter eggs than the other two populations ($F_{2,60} = 10.6$, $P < 0.001$). Proximate composition of the eggs was quite similar among the populations (Table 3.1). There were no differences among the populations in the proportion of fat ($F_{2,62} = 1.3$, $P = 0.29$), lean mass ($F_{2,62} = 3.1$, $P = 0.05$), or water ($F_{2,62} = 1.6$, $P = 0.22$). Similarly, fat content on a dry mass basis did not differ among the populations ($F_{2,62} = 2.8$, $P = 0.07$) nor did the lean mass ($F_{2,62} = 2.8$, $P = 0.07$).

*Egg Fatty Acid Composition*

We identified twenty fatty acids in the Chinook salmon eggs (Table 3.2). Of these fatty acids, 16:0, 18:1(n-9), 18:1(n-7), 20:5(n-3), and 22:6(n-3) were particularly abundant in the eggs of all three populations. PCA revealed that the populations differed in egg fatty acid composition (Figure 3.1). The first five principal components (PCs) had eigenvalues > 1 and explained 79% of the variation (Table 3.3). For PC1, there was high positive loadings for the PUFAs, and negative loadings for SFAs and monounsaturated fatty acids (MUFAs). PC2 had a strong positive loading for 22:5(n-3) and high negative loadings for 14:0, 16:1(n-7), 16:1(n-9), and 20:1(n-9). PC3 had high positive loadings for 18:2(n-6) and 18:3(n-3), and a strong negative loading for 22:6(n-3). PC4 had strong

positive loadings for 20:3(n-6), 16:2(n-4), and a strong negative loading for 16:0. Finally, PC5 had a strong positive loading for 20:4(n-6) and strong negative loadings for 20:1(n-9), 20:2(n-6), 20:3(n-3) and 20:3(n-6).

Of the retained PCs, there were differences among populations for PC1 ($F_{2,62}$ = 46.9, P < 0.001), PC3 ($F_{2,62}$ = 9.2, P < 0.001), and PC4 ($F_{2,62}$ = 3.7, P = 0.03), whereas there were no differences among populations for PC2 ($F_{2,62}$ = 1.3, P = 0.28) or PC5 ($F_{2,62}$ = 1.0, P = 0.39). The most striking difference was along PC1, where eggs from the Credit River had a higher proportion of n-3 PUFAs and eggs from the Pine River had a higher proportion of SFAs and MUFAs (Figure 3.1). The fatty acid profiles of Sydenham River eggs fell between the extremes of the Credit and Pine River.

Only PC1 was considered in models of growth/size and survival for two reasons. First, PC1 explained 38.6% of the variation in fatty acid composition, which was much higher than the other PC axes (Table 3.3). Second, the inclusion of additional PC axes in the analysis would result in a full model that was over parameterized. Prior to using PC1 as predictor variable, I tested for any correlations between PC1 and egg mass within the populations and found that they were only weakly correlated (Credit: r = 0.29, P = 0.03; Pine: r = 0.38, P < 0.001; Sydenham: r = 0.29, P = 0.02).

*Hatch Length*

Hatch length was influenced by all the egg quality covariates; however, the covariates were involved in several two-way interactions with temperature and population (Table 3.4; Appendix B.4). Temperature had a large effect on hatch length and there was a marked decreased in length at 15.2°C (Figure 3.2). Hatch length was affected by a temperature x PC1 interaction ($\chi_2^2$ = 7.34, P = 0.03), whereby the relationship between PC1 and hatch length was positive at 6.5°C, but close to zero at 9.4°C and 15.2°C (Figure 3.2). The relationship between hatch length and PC1 varied across populations with the Credit River having a positive slope and the Pine and Sydenham Rivers having a negative slope (population x PC1: $\chi_2^2$ = 8.54, P = 0.01; Figure 3.2). The quantity of lipid also influenced hatch length with the Pine River having a positive slope and the Credit and Sydenham Rivers having a negative slope (population x lipid: $\chi_2^2$ =

13.76, P = 0.001; Appendix B.4). Finally, hatch length was positively related to egg mass in all populations, but the strength of the relationship varied among populations (population x egg mass: $\chi_2^2$ = 15.65, P < 0.001; Appendix B.4).

*Swim-Up Length*

Swim-up length was influenced by egg mass and PC1, but the relationships depended on population and temperature (Table 3.4; Appendix B.5). Egg mass was positively related to swim-up length and the slope of the relationship depended on population (population x egg mass: $\chi_2^2$ = 38.49, P < 0.001) and temperature (temperature x egg mass: $\chi_2^2$ = 20.21, P < 0.001; Appendix B.5). PC1 influenced swim-up length differently among the populations with the Credit River having a positive slope and the Pine and Sydenham Rivers having a negative slope (population x PC1: $\chi_2^2$ = 32.14, P < 0.001; Figure 3.3). Swim-up length also varied by population and temperature ($\chi_4^2$ = 73.22, P < 0.001; Appendix B.5).

*Growth Rate*

Growth rate was affected by interactions involving egg mass and lipid content (Table 3.4; Appendix B.6). The relationship between growth rate and lipid content varied by population (population x lipid: $\chi_2^2$ = 8.40, P < 0.02) and temperature (temperature x lipid: $\chi_2^2$ = 13.95, P < 0.001; Figure 3.4). The positive relationship between growth rate and lipid content was stronger for the Credit River than both the Pine and Sydenham Rivers. Furthermore, the slope of the growth rate - lipid relationship increased with temperature treatment, whereby the steepest relationship was present at 15.2°C (Figure 3.4). Egg mass was also positively related to growth rate and the slope of the relationship varied across populations with the Pine River having the greatest slope and the Sydenham having the weakest slope (population x egg mass: $\chi_2^2$ = 6.63, P = 0.04; Appendix B.6). Growth rate also varied by population and temperature ($\chi_4^2$ = 61.45, P < 0.001; Appendix B.6).

*Survival Traits*

The median survival ranged from 93.4% – 100% and 96.0% - 100% for hatch success and hatch to swim-up survival, respectively (Appendix B.2). The high survival is most notable for hatch to swim-up survival, where many families experienced 100% survival. I did not perform model selection or interpret the results from the survival models for two reasons. First, there was very little variation in survival to explain with the models. Second, the full model for hatch success had poor predictive performance with a conditional $R^2$ of 0.23 (highest $R^2$ achieved). Taken together, the hatch success and hatch to swim-up survival models did not provide biologically meaningful results.

**Table 3.1:** Female length, egg wet mass, and egg proximate composition of Chinook salmon (*Oncorhynchus tshawytscha*) collected in the Credit (n=18), Pine (n=26) and Sydenham Rivers (n=21). Values are presented as mean ± standard error and calculated from family level data.

| | **Credit River** | **Pine River** | **Sydenham River** |
|---|---|---|---|
| **Female Trait** | | | |
| Fork Length (cm) | 88.93 ± 1.62 | 74.51 ± 1.26 | 75.78 ± 1.43 |
| **Egg Trait** | | | |
| Wet mass (g) | 0.284 ± 0.011 | 0.177 ± 0.007 | 0.207 ± 0.008 |
| *Wet Mass Composition* | | | |
| Lipid ($g \cdot g$ wet $mass^{-1}$) | 0.076 ± 0.003 | 0.074 ± 0.002 | 0.071 ± 0.002 |
| Lean mass ($g \cdot g$ wet $mass^{-1}$) | 0.469 ± 0.005 | 0.479 ± 0.006 | 0.490 ± 0.005 |
| Water ($g \cdot g$ wet $mass^{-1}$) | 0.455 ± 0.006 | 0.447 ± 0.006 | 0.439 ± 0.006 |
| *Dry Mass Composition* | | | |
| Lipid ($g \cdot g$ dry $mass^{-1}$) | 0.139 ± 0.004 | 0.132 ± 0.003 | 0.127 ± 0.003 |
| Lean mass ($g \cdot g$ dry $mass^{-1}$) | 0.861 ± 0.004 | 0.868 ± 0.003 | 0.873 ± 0.003 |

**Table 3.2:** Mean percentage (± standard error) of individual fatty acids, fatty acid families, and fatty acid ratios in Chinook salmon (*Oncorhynchus tshawytscha*) eggs collected from the Credit, Pine and Sydenham Rivers.

| Fatty Acid | **Credit River (n=18)** | **Pine River (n=26)** | **Sydenham River (n=21)** |
|---|---|---|---|
| **Saturated** | | | |
| 14:0 | 2.1 ± 0.3 | 1.3 ± 0.2 | 2.0 ± 0.1 |
| 16:0 | 14.1 ± 0.4 | 15.5 ± 0.4 | 16.1 ± 0.4 |
| 18:0 | 5.8 ± 0.3 | 7.7 ± 0.3 | 7.3 ± 0.2 |
| **Monounsaturated** | | | |
| 16:1(n-9) | 1.2 ± 0.1 | 1.0 ± 0.1 | 1.1 ± 0.1 |
| 16:1(n-7) | 5.6 ± 0.2 | 7.9 ± 0.4 | 7.6 ± 0.3 |
| 18:1(n-9) | 22.1 ± 0.5 | 27.3 ± 0.5 | 23.9 ± 0.7 |
| 18:1(n-7) | 5.2 ± 0.2 | 8.0 ± 0.3 | 7.2 ± 0.3 |
| 20:1(n-9) | 0.8 ± 0.1 | 0.7 ± 0.1 | 0.9 ± 0.1 |
| **Polyunsaturated n-3** | | | |
| 18:3(n-3) | 4.7 ± 0.2 | 1.8 ± 0.1 | 1.8 ± 0.1 |
| 18:4(n-3) | 1.2 ± 0.1 | 0.6 ± 0.1 | 0.6 ± 0.1 |
| 20: 3(n-3) | 1.1 ± 0.1 | 0.5 ± 0.1 | 0.7 ± 0.2 |
| 20:4(n-3) | 3.2 ± 0.1 | 1.5 ± 0.1 | 1.9 ± 0.1 |
| 20:5(n-3) | 8.0 ± 0.3 | 5.5 ± 0.2 | 6.3 ± 0.2 |
| 22:5(n-3) | 3.3 ± 0.2 | 2.8 ± 0.1 | 3.2 ± 0.2 |
| 22:6(n-3) | 8.9 ± 0.6 | 7.6 ± 0.4 | 8.9 ± 0.5 |
| **Polyunsaturated n-4** | | | |
| 16:2(n-4) | 0.4 ± 0.1 | 0.4 ± 0.1 | 0.3 ± 0.1 |
| **Polyunsaturated n-6** | | | |
| 18:2(n-6) | 5.1 ± 0.1 | 4.1 ± 0.2 | 3.8 ± 0.1 |
| 20:2(n-6) | 0.7 ± 0.1 | 0.5 ± 0.1 | 0.6 ± 0.1 |
| 20:3(n-6) | 0.4 ± 0.1 | 0.4 ± 0.1 | 0.4 ±0.1 |
| 20:4(n-6) | 6.0 ± 0.2 | 5.1 ± 0.2 | 5.3 ± 0.1 |
| Σ SFA | 21.9 ± 0.7 | 24.5 ± 0.5 | 25.4 ± 0.6 |
| Σ MUFA | 34.8 ± 0.8 | 44.8 ± 0.7 | 40.6 ± 1.0 |
| Σ PUFA | 43.1 ± 1.4 | 30.6 ± 0.7 | 33.8 ± 1.2 |
| Σ PUFA n-3 | 30.5 ± 1.2 | 20.2 ± 0.6 | 23.4 ± 1.0 |
| Σ PUFA n-6 | 12.3 ± 0.3 | 10.1 ± 0.2 | 10.2 ± 0.2 |
| n-3:n-6 | 2.5 ± 0.1 | 2.0 ± 0.1 | 2.3 ± 0.1 |
| DHA:EPA | 1.1 ± 0.1 | 1.4 ± 0.1 | 1.4 ± 0.1 |

**Table 3.3:** Factor loadings for the first 5 principal components from a principal components analysis on the fatty acid composition of eggs from the Credit, Pine and Sydenham Rivers.

| | PC1 | PC2 | PC3 | PC4 | PC5 |
|---|---|---|---|---|---|
| **Saturated** | | | | | |
| 14:0 | 0.04 | -0.49 | -0.02 | -0.14 | 0.17 |
| 16:0 | -0.20 | -0.04 | 0.16 | -0.45 | 0.05 |
| 18:0 | -0.27 | 0.20 | 0.035 | -0.12 | -0.13 |
| **Monounsaturated** | | | | | |
| 16:1(n-9) | 0.08 | -0.37 | 0.02 | 0.16 | 0.15 |
| 16:1(n-7) | -0.24 | -0.30 | -0.10 | -0.01 | 0.24 |
| 18:1(n-9) | -0.26 | -0.04 | 0.09 | 0.24 | -0.27 |
| 18:1(n-7) | -0.29 | 0.11 | -0.18 | 0.19 | -0.15 |
| 20:1(n-9) | 0.12 | -0.32 | -0.26 | -0.16 | -0.46 |
| **Polyunsaturated n-3** | | | | | |
| 18:3(n-3) | 0.28 | 0.09 | 0.36 | -0.03 | 0.09 |
| 18:4(n-3) | 0.26 | -0.28 | 0.12 | 0.14 | 0.05 |
| 20:3(n-3) | 0.23 | -0.07 | 0.14 | -0.09 | -0.31 |
| 20:4(n-3) | 0.30 | 0.13 | 0.24 | -0.08 | -0.13 |
| 20:5(n-3) | 0.31 | 0.01 | -0.10 | -0.05 | 0.26 |
| 22:5(n-3) | 0.23 | 0.31 | -0.29 | 0.01 | -0.05 |
| 22:6(n-3) | 0.23 | 0.19 | -0.42 | -0.07 | 0.09 |
| **Polyunsaturated n-4** | | | | | |
| 16:2(n-4) | 0.02 | -0.17 | 0.050 | 0.59 | 0.11 |
| **Polyunsaturated n-6** | | | | | |
| 18:2(n-6) | 0.18 | 0.15 | 0.50 | 0.09 | -0.07 |
| 20:2(n-6) | 0.22 | -0.28 | -0.11 | -0.20 | -0.40 |
| 20:3(n-6) | 0.13 | 0.05 | -0.16 | 0.43 | -0.31 |
| 20:4(n-6) | 0.25 | 0.09 | -0.28 | 0.01 | 0.30 |
| **Eigenvalue** | 7.71 | 2.84 | 2.16 | 1.68 | 1.37 |
| **Variance Explained (%)** | 38.6 | 14.2 | 10.8 | 8.4 | 6.8 |

**Table 3.4:** Parameters, marginal $R^2$, and conditional $R^2$ of the hatch length (HL), swim-up length (SL), and growth rate (GR) models. Parameters included in the models were population (P), temperature (T), egg mass (EM), PC1 score, and lipid content (L). Two-way interactions between the variables are denoted with an asterisk. The random effect of sire was included in all models. The marginal $R^2$ and conditional $R^2$ represent the variance explained by the fixed effects and the full model, respectively.

| Trait | Parameters | $R_M^2$ | $R_C^2$ |
|---|---|---|---|
| HL | μ + P + T + EM + PC1 + L + P*EM + P*PC1 + T*PC1 + P*L | 0.91 | 0.92 |
| SL | μ + P + T + EM + PC1 + P*EM + T*EM + P*T + P*PC1 | 0.90 | 0.97 |
| GR | μ + P + T + EM + L + P*EM + P*T + T*L + P*L | 0.59 | 0.68 |

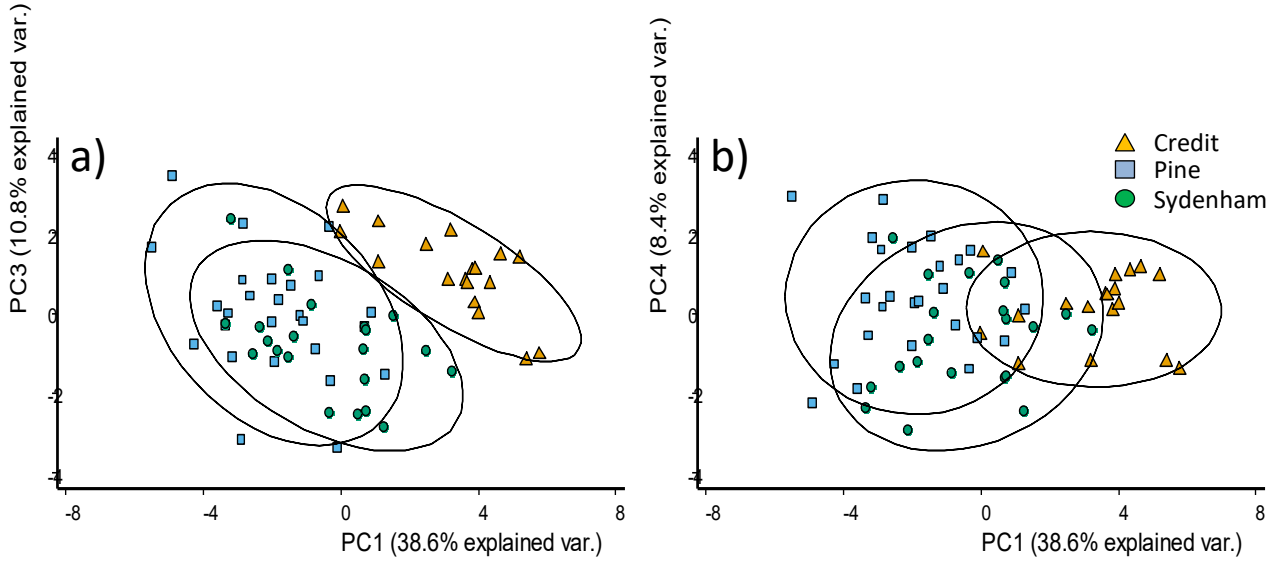


**Figure 3.1:** Scatterplots of (a) principal component 1 and 3, and (b) principal component 1 and 4 from a principal component analysis of Chinook salmon (*Oncorhynchus tshawytscha*) egg fatty acid composition among the Credit, Pine, and Sydenham Rivers. The ellipses are the 95% confidence ellipses for the populations.

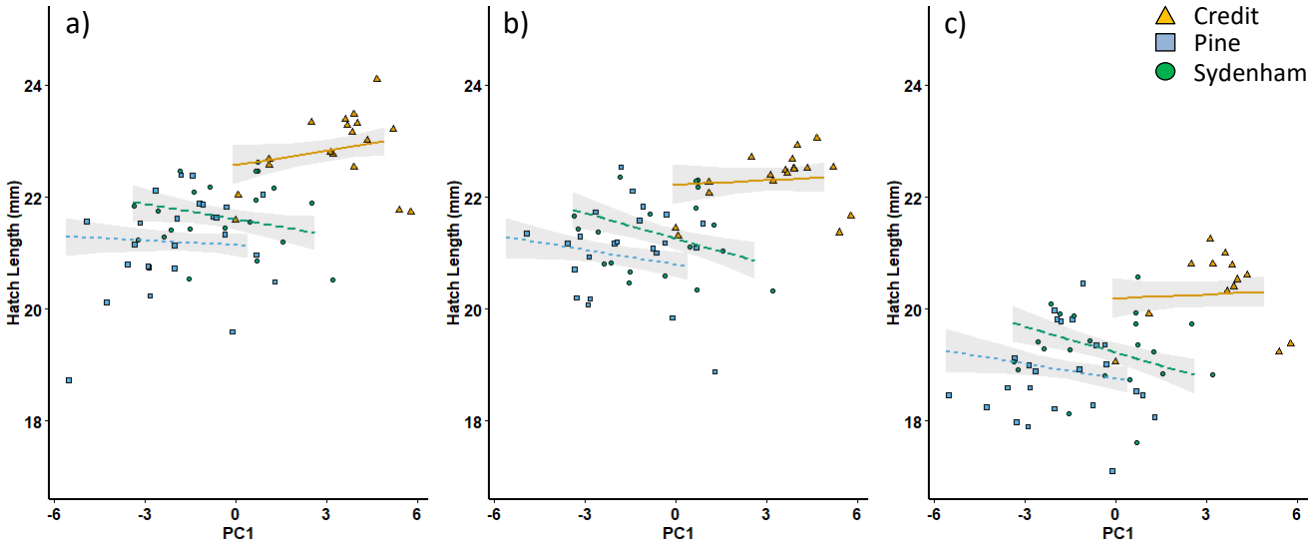


**Figure 3.2:** Relationship between hatch length and PC1 at a) 6.5°C, b) 9.4°C, and c) 15.2°C from a linear mixed model. Egg mass and lipid content were set at their respective population level mean values. Shaded regions around each regression line represent the 95% confidence interval estimated using parametric bootstrapping.

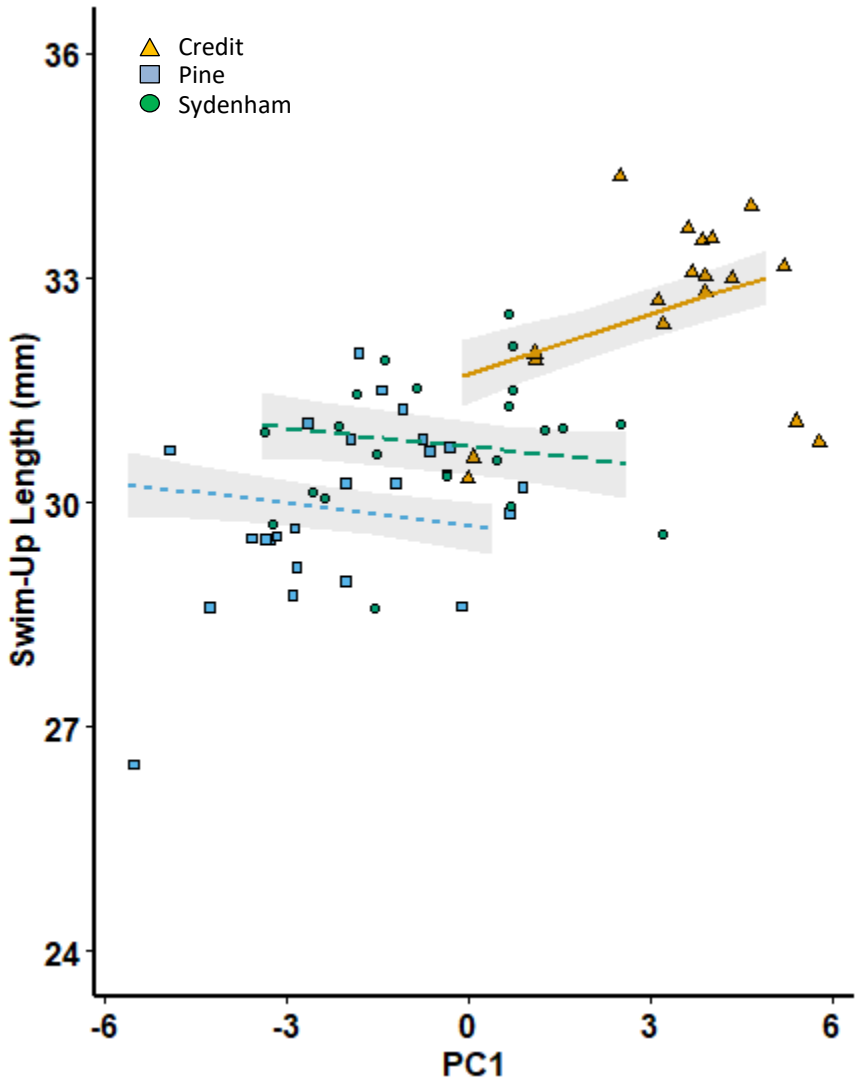


**Figure 3.3:** Relationship between swim-up length and PC1 from a linear mixed model. Egg mass was set at their respective population means, while temperature was set at 6.5°C. Shaded regions around each regression line represent the 95% confidence interval estimated using parametric bootstrapping.

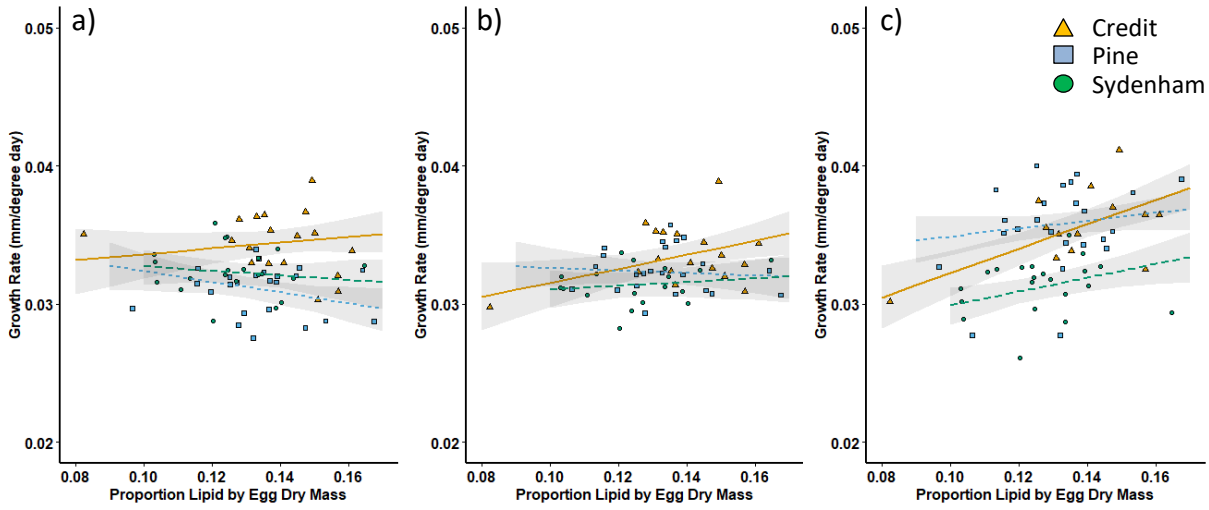


**Figure 3.4:** Relationship between growth rate and egg lipid content at a) 6.5°C, b) 9.4°C, and c) 15.2°C from a linear mixed model. Egg mass and PC1 scores were set at their respective population level mean values. Shaded regions around each regression line represent the 95% confidence interval estimated using parametric bootstrapping.

## 3.4 Discussion

In this study, I show that there are transgenerational effects of maternal diet, expressed as variation in egg nutrient content, on the development of Chinook salmon progeny reared under three different temperatures. The egg nutrient component involved in the transgenerational effect varied among traits, where hatch length was affected by both the fatty acid composition (PC1 axis) and lipid content, swim-up length was affected by fatty acid composition, and growth rate was affected by lipid content. Importantly, the relationship between the traits and egg nutrient content was dependent on population and/or temperature. Egg wet mass and temperature were more important predictors than the egg nutrient content for all the traits, regardless of developmental stage (t-values: Appendix B.4-B.6).

Hatch and swim-up length were influenced by an interaction between fatty acid composition and population, where eggs with a high PUFA content achieved the largest length in the Credit River and eggs with a high SFA and MUFA content achieved the largest length in the Lake Huron populations (Pine and Sydenham Rivers). The presence of a population x fatty acid composition interaction suggests that the metabolism of each population is adapted to the forage base available to mothers during egg development. If the developing offspring used fatty acids in the same way regardless of population (i.e., no divergence), then we would expect to see all three populations achieve the largest length with a similar egg fatty acid composition. Instead, we see the largest offspring lengths achieved with egg fatty acid compositions that reflect those available in their population of origin (i.e., maternal forage base). Such divergence in metabolism could be due to variation in the selective use of fatty acids for energy, where the Credit River population relies heavily on PUFAs (e.g., DHA and EPA) and the Lake Huron populations rely heavily on SFAs (e.g., 16:0) and MUFAs (e.g., 18:1(n-9); Tocher, 2003). If true, this divergence in metabolism has occurred ~ 10 generations since the populations were first introduced to the Great Lakes from a common genetic source (Thorn & Morbey, 2018). Similar metabolic divergence has been found within an aquaculture setting where a domesticated strain of coho salmon (*Oncorhynchus kisutch*) had a significantly greater feed conversion efficiency relative to its source population after 16

generations (Neely, Myers, Hard, & Shearer, 2008). The connection between offspring metabolism and maternal diet, via egg fatty acid content, could be the result of selection acting directly on offspring metabolism or a correlated response to selection acting on adult metabolism. However, further research is required to determine the metabolic and evolutionary mechanisms behind the among population variation in fatty acid use during development.

Hatch length was also affected by an interaction between temperature and fatty acid composition. Consistent with my prediction, there was a positive relationship between hatch length and the relative quantity of PUFAs at 6.5°C and a very weak relationship at 9.4°C and 15.2°C. The positive relationship between hatch length and the relative quantity of PUFAs in the cold temperature treatment is likely related to the temperature sensitivity of membrane function and metabolism to fatty acid composition (Hazel, 1984, 1995; Robertson & Hazel, 1997). At cold temperatures, PUFAs are selectively incorporated into cell membranes to maintain membrane function (Craig, Neill, & Gatlin, 1995; Ma, Qiang, He, Gabriel, & Xu, 2015; Snyder, Schregel, & Wei, 2012). Furthermore, the digestibility of PUFAs is maintained at low temperature, whereas it is reduced for SFAs, making PUFAs a preferred source of energy for growth at low temperature (Olsen & Ringo, 1998). Offspring hatching from eggs with a higher quantity of PUFAs would be capable of attaining a larger size before depleting their reserve of PUFAs (Hazel, 1995). The developmental advantage of having lipid reserves rich in PUFAs would be reduced with increasing temperature as other fatty acids are more efficiently utilized, which is consistent with the lack of a hatch length – PUFA relationship at higher temperatures.

Growth rate increased with the proportion of lipid in an egg and, as predicted, the relationship depended on the rearing temperature. The positive percent lipid – growth rate relationship was only present at 15.2°C and not in the colder treatments. The appearance of a percent lipid-growth rate relationship at high temperature is related to the temperature dependence of metabolism in ectotherms. As temperature increases, metabolic rate increases (Schulte, 2015) and conversion efficiency is reduced (Heming, 1982; Kullgren et al., 2013; Rombough, 1994). The combined effects of higher metabolic

rate and reduced conversion efficiency at high temperature puts a greater energetic demand on the endogenous energy resources of developing larvae. This increased energy demand at high temperature can deplete lipid stores prior to swim-up or compromise the development of larvae with small stores leading to reduced survival for these individuals (Fisher, Sogard, & Berkeley, 2007). Furthermore, offspring provided with less lipid stores appear to have reduced growth rates relative to offspring with large lipid stores at high temperature, which can lead to reduced offspring size at emergence. It is possible that females able to invest more lipids into their eggs will have a better fitness in warmer temperatures.

Variation in the fatty acid composition of the eggs most likely reflects dietary differences among the Great Lakes Chinook salmon populations. The Credit River eggs tended to have a higher proportion n-3 PUFAs, whereas the Lake Huron populations had more SFAs and MUFAs. The difference between the Lake Ontario (Credit River) eggs and the Lake Huron (Pine and Sydenham Rivers) eggs is not surprising given that they are from lake systems with a different prey fish composition (Bunnell et al., 2014). Chinook salmon in the Great Lakes preferentially prey upon alewife (Diana, 1990; Happel, Pattridge, Walsh, & Rinchard, 2017; Jacobs, Madenjian, Bunnell, Warner, & Claramunt, 2013; Warner, Kiley, Claramunt, & Clapp, 2008) and the abundance of alewife in 2012, when our fish were collected, differed between Lakes Huron and Ontario (Ontario Ministry of Natural Resources and Forestry, 2013; Warner, O'Brien, Farha, Schaeffer, & Lenart, 2013). In Lake Huron, the alewife abundance was unusually low and unlikely to make any significant contribution to the diet of Chinook salmon (Warner et al., 2013), whereas the alewife abundance in Lake Ontario was much greater (OMNRF, 2013). Furthermore, alewife tend to have higher concentrations of n-3 and n-6 PUFAs relative to other prey fish in the Great Lakes (Honeyfield et al., 2012). Taken together, differences in the contribution of alewife to the diet of Chinook salmon likely accounts for much of the difference in the fatty acid composition we found between the lake systems.

Within Lake Huron, I also found differences in the fatty acid composition of eggs from the Sydenham River and Pine River females. Recent work by Marklevitz et al.

(2016) suggests that there is regional structuring of Chinook salmon in Lake Huron. The Pine and Sydenham Rivers are both located in southern Georgian Bay and our results suggest that there is a possibility of fine scale, population-level structuring of Chinook salmon in Lake Huron. Vitellogenesis occurs over a period of months (Tyler & Sumpter, 1996; Tyler, Sumpter, & Witthames, 1990) and the fatty acid composition of eggs will integrate dietary signals over this period (Pickova, Kiessling, Pettersson, & Dutta, 1999). Therefore, the differences I found between the Pine and Sydenham Rivers only partially reflect dietary differences due to spatial variation during pre-spawning staging and will also reflect spatial variation while actively feeding within the main basin of the lake.

The transgenerational effects of maternal egg nutrient allocation on offspring development has several potential management implications. The forage base available to mothers during the period of vitellogenesis will have a direct influence on the composition of lipids deposited as yolk (Johnson, 2009; Pickova et al., 1999; Wiegand, 1996). Thus, the lipid composition of Chinook salmon eggs will track shifts in the prey fish community among regions and/or years and, depending on the environmental context, could be an important unaccounted source of spatial-temporal variation in juvenile recruitment. In addition, anthropogenic climate change is poised to increase water temperatures in lakes and rivers around the globe (Isaak, Wollrab, Horan, & Chandler, 2012; O'Reilly et al., 2015; Punzet, Voß, Voß, Kynast, & Bärlund, 2012), including the Great Lakes watershed (Trumpickas, Shuter, & Minns, 2009). Higher water temperatures during endogenous feeding will increase the amount of energy per offspring required for development. This shift in the cost of early life history development could reduce the productivity of Chinook salmon, along with other salmonids, in the Great Lakes unless females compensate by allocating more energy, on a relative basis, to each offspring. Finally, the fatty acid composition of eggs can serve as a trophic biomarker and used to better understand the foraging habitats of a specific population (Happel et al., 2016). Before we can fully understand any management implications, however, more research needs to be done on the connection between transgenerational effects of maternal diet, success during juvenile life history stages, and population dynamics.

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# 4 Survival under the gravel: the effects of egg size and parental identity on the in-situ hatching success of Chinook salmon (*Oncorhynchus tshawytscha*)

## 4.1 Introduction

The successful management or restoration of a population requires knowledge of where production bottlenecks occur, both developmentally and spatially, and what factors are associated with these high mortality events. For salmon, production bottlenecks may occur at any developmental stage (Cantin & Post, 2018); however, some of the highest mortality is often incurred during the early life history stage of development because individuals tend to be more vulnerable to predation, starvation, and environmental variation (Houde, 1989, 1994; Leggett & Deblois, 1994; Pepin, 1991). The factors affecting survival during early life can be broadly categorized as extrinsic (i.e., environmental) or intrinsic (i.e., genetic or parental effects). Most studies investigating salmonid early life survival in the wild have focused on the effect of extrinsic factors, while ignoring intrinsic factors (Bennett, Connor, & Eaton, 2003; Jensen, Steel, Fullerton, & Pess, 2009; Malcolm, Youngson, Soulsby, Imholt, & Fryer, 2011; Malcolm, Youngson, & Soulsby, 2003; Stark, Vidergar, Kozfkay, & Kline, 2018). Laboratory studies have shown that intrinsic factors can greatly affect early life survival in salmonids either independently or through an interaction with extrinsic factors (Einum, Hendry, & Fleming, 2002; Heath, Fox, & Heath, 1999; Houde, Wilson, & Neff, 2013; Rollinson, Hutchings, & Fleming, 2011). However, a laboratory is a relatively simplistic rearing environment that is unlikely to adequately represent the complex natural environment.

The survival of developing embryos within a redd has been linked to a variety of environmental variables, including substrate composition, dissolved oxygen (DO), scour, and temperature. The quantity of fine sediment (< 4 mm in diameter) within the redd environment has been found to greatly affect the survival of developing embryos (Chapman, 1988; Jensen et al., 2009). Fine sediment can reduce the intragravel flow of water through a redd, which can lead to hypoxic/anoxic conditions in the egg pocket (Chapman, 1988; Greig, Sear, & Carling, 2007). Fine sediment can also form a barrier

within a redd that prevents fry from emerging and free feeding (entombment; Witzel and MacCrimmon 1981, Chapman 1988). Low DO concentrations within the egg pocket of a redd can occur for a variety of reasons, such as the infiltration of oxygen poor groundwater, excessive fine sediment, or sediment with a high oxygen demand (Greig et al., 2007), and has been found to negatively affect the survival and development of salmonid embryos (Malcolm et al., 2011; Malcolm et al., 2003). High riverine flows or ice can scour the substrate of tributaries and destroy entire redds, which has been shown to be a large source of early life mortality in some systems (Cunjak & Therrien, 1998; Gauthey et al., 2017). Given that salmon are ectotherms, the survival of embryos is also affected by temperature, whereby mortality can be high when the temperature falls outside of the upper or lower lethal limits of the population (Pepin, 1991; Richter & Kolmes, 2005).

How an individual embryo responds to environmental conditions within a redd can depend on its egg size, which is a maternally controlled parental effect (i.e., maternal effect). For many years, researchers hypothesized that small eggs perform better in low oxygen environments (e.g., high sand content in redd) relative to large eggs because small eggs have a higher surface area to volume ratio and are likely more efficient at transporting oxygen into the egg (Quinn, Hendry, & Wetzel, 1995). More recently, however, direct measurements of oxygen demand relative to egg size has shown that large eggs perform better in oxygen limited environments because metabolic oxygen demand increases relatively slowly with egg size (Einum et al., 2002). Egg size has been shown to interact with temperature to affect salmonid early life survival, whereby embryos from small eggs have a greater survival probability than those from large eggs at high temperatures (Régnier, Bolliet, Gaudin, & Labonne, 2013). The gravel composition of a redd can also interact with egg size to influence alevin development, where offspring from large eggs tend to emerge under-developed from redds composed of small gravels (Rollinson et al., 2011). Though it seems clear that egg size can influence the survival of developing embryos, these interactions between environmental variables and egg size were derived in a laboratory and it is unclear how they may manifest in the wild to shape survival outcomes for individuals derived from different egg sizes.

Other intrinsic factors beyond egg size can also influence early life history survival in salmonids. These additional intrinsic factors can be maternally controlled traits, such as egg nutrient content, or genetic effects (Falconer & Mackay, 1996; Lynch & Walsh, 1998). The variance of a phenotype can be partitioned into maternal or genetic effects using a quantitative genetic breeding design (Lynch & Walsh, 1998). Quantitative genetic studies conducted in a hatchery have found that early life history traits, such as growth and survival, are often most influenced by maternal effects rather than genetic effects (Heath et al., 1999; Houde et al., 2013; Thorn & Morbey, 2018). The relative importance of genetic and maternal effects depends on the rearing environment (Charmantier & Garant, 2005; Hoffmann & Merilä, 1999) and observations from a benign selection environment like a hatchery may not apply to natural conditions.

Few studies have investigated intrinsic factors and early life survival in the wild (Einum & Fleming, 2000; Gauthey et al., 2017; Johnson, Roni, & Pess, 2012; Roni et al., 2016). Egg size appears to have mixed effects on in-situ survival, which range from no effect (Gauthey et al., 2017) to a positive relationship (Einum & Fleming, 2000), and no interactions between egg size and extrinsic factors have been found (Gauthey et al., 2017). More broadly, parentage has been found to influence early life survival in the wild with the strength of the parentage effect varying over years (Johnson et al., 2012; Roni et al., 2016). Such a parentage effect incorporates egg size, genetic, and maternal effects and provides little detail about how specific intrinsic factors influence survival. Based on the existing in-situ studies, egg size effects appear to be variable among populations and more complicated than predicted from hatchery-based observations (i.e. no egg size – extrinsic factor interactions). Furthermore, no studies have quantified the relative importance of egg size, genetic, and parental effects to early life survival of salmonids in the wild. Understanding what sources of variation contribute to early life survival in the wild has important implications for the selection of breeders and/or source populations for hatchery programs (Pitcher & Neff, 2007), for predicting how a population will respond to selection (Garcia de Leaniz et al., 2007), and for predicting population dynamics (i.e., production; Venturelli et al. 2010).

For this study, I reared embryos from three Great Lakes Chinook salmon (*Oncorhynchus tshawytscha*) populations in their natal spawning tributaries and a hatchery to address four research objectives: 1) to assess the effect of egg mass and parental effects on the hatching success of Chinook salmon reared in the wild; 2) to assess the influence of redd gravel composition, a primary extrinsic effect, and its interaction with egg mass on hatching success in the wild; 3) to determine whether egg mass – survival relationships have population-level consequences in the wild; 4) to determine if results from hatchery studies translate to the wild. I did this by rearing embryos from the three Chinook salmon populations in a hatchery until the eyed-up stage of development. I then transferred half the embryos from each family to their respective river of origin and reared them in-situ and retained the other half in the hatchery. The number of surviving alevins at ~15 days post hatch was used to calculate egg-to-alevin survival and estimate egg mass – survival relationships for each population. Finally, we ran a simulation analysis using the in-situ egg mass – survival relationships to determine how changes in egg mass distributions within each population could influence the relative number of surviving alevins produced by a population.

## 4.2 Materials and Methods

*Study Sites and Egg Collection*

Gametes were collected from three Chinook salmon populations in the Laurentian Great Lakes: 1) Credit River; 2) Pine River; and 3) Sydenham River (Figure 4.1). Adult salmon were captured in the Credit River using a backpack electrofisher on 01 October 2012, in the Pine River using a combination of dip and seine nets from 19-27 September 2012, and in Sydenham River using a fish trap built into the Mill Street Dam from 22 September – 06 October 2012. All captured individuals were checked for sexual maturity by gently massaging the abdomen and, if gametes were freely released, a sample of ~500 eggs or a few millilitres of milt was collected. Sampled individuals were also measured for fork length and released after capture (exception: Credit River individuals were retained by the OMNRF as hatchery stock). We did not remove gametes from visibly unhealthy individuals. The collected egg and milt samples were transported to the Western University experimental hatchery in a cooler kept ~4°C. All fish collection and

husbandry protocols were approved by the Western University Animal Care Subcommittee (2007-043-05).

*Hatchery Rearing*

Gametes from each population were fertilized using a half-sib, full-sib breeding design, whereby one male was crossed with two females from the same population. The fertilizations produced 20 Credit River, 21 Sydenham River, and 22 Pine River families. The eggs from each family were split into two groups: 1) 80 eggs from each family were reared in the hatchery until 15 days post hatch; and 2) 100 eggs from each family were reared in the hatchery up to the eyed-up stage and then transferred to their natal tributaries until 15 days post hatch. The hatchery group was held at a mean (± SD) temperature of 6.5°C (± 0.8), which was the coldest temperature we could achieve in the hatchery and was used to mimic the mean temperature these fish would experience in the wild (Thorn & Morbey, 2018). The in-situ group was held in the hatchery at a mean (± SD) temperature of 9.4°C (± 0.3) until the eyed-up stage, which is when an observer can clearly see the dark eye pigment of the embryos. These individuals were held at 9.4°C because it was close to the temperature they would have experienced in the wild between fertilization and the eyed-up stage (Thorn & Morbey, 2018). Families reared in the wild were likely to experience increased mortality rates and, as such, I allocated more individuals to the in-situ group.

Eggs from each family and rearing group were allocated equally to two egg cups for hatchery rearing (40/50 eggs per cup; 6 cm diameter x 5 cm height) and held in upwelling incubation trays. The developing embryos were monitored daily and all dead embryos (i.e., white in colour) were removed to prevent disease. All removed embryos were preserved in Stockard's solution and later assessed for evidence of fertilization (Boyd, Oldenburg, & McMichael, 2010). The hatchery group remained in the egg cups until 15 days post hatch.

*In-Situ Rearing*

I identified areas of salmon spawning habitat by visiting each river and locating active sites of redd creation and occupation. I then used these spawning surveys to choose 2-3 incubator sites in each river (Figure 4.1).

When embryos from the in-situ group reached the eyed-up stage, they were counted, transferred to water filled containers, and placed in a cooler maintained at ~10°C for transport to their river of origin for placement in incubators and artificial redds. The eyed-up stage of development was chosen because embryos at this stage of development have been found to be robust to handling and transport (Jensen & Alderdice, 1983, 1989). Timing of the eyed-up stage was highly synchronous among families fertilized on the same day and these families were transferred to the river in blocks.

Incubators were modelled after MacCrimmon et al. (1989) with some application specific modifications (Figure 4.2). Incubators were constructed with 11 cm diameter PVC tubing cut to a length of 27 cm. Two large windows were cut into the sides of the incubators and covered with 4 mm aquaculture grade mesh, which was small enough to retain hatched alevins and large enough to allow fine sediment to enter the incubator. One end of the incubator was permanently sealed using a PVC end cap with adhesive, while the other end was sealed in the field using a pressure fitted PVC end cap.

At the site of installation, I constructed artificial redds one-at-a-time by digging a depression in the gravel substrate (Figure 4.2). Incubators were filled with site specific gravel that was sieved to remove all sediment < 4 mm in diameter. This gravel fraction was removed to mimic the winnowing of fine sediment that occurs during female nest construction (Quinn, 2005) and to allow us to estimate the accumulation of fine sediment within the egg pocket during the study (window mesh allows sediment < 4 mm through). The gravel was placed in the incubator and the eyed embryos were gently transferred into the middle of the incubator using a plastic tube (Figure 4.2). The plastic tube was slowly removed, and the incubator was filled to the top with some additional gravel. The incubator was sealed with an end cap and placed in the artificial redd so that the egg pocket was approximately 22 cm below the gravel, which is within the range of egg

burial depths for Chinook salmon in the wild (DeVries, 1997; Figure 4.2). The incubators were then covered with gravel in the form of a salmon redd (Figure 4.2). Cable ties looped through the top of the incubator stuck up through the gravel surface of the redd so that the incubator could be easily re-located at the end of the study. I also installed one environmental incubator containing a HOBO temperature logger instead of eggs at each site following the same protocol as incubators containing embryos. I paired this incubator temperature logger with a HOBO temperature logger installed just above the gravel surface.

Incubators were removed from the stream when the embryos reached ~ 15 days post-hatch. I collected temperature readings from the surface HOBO temperature logger at each site weekly and used a temperature-dependent growth equation from Jensen et al. (2009) to predict when the developing embryos reached ~ 15 days post-hatch. Incubators were removed by carefully excavating around each incubator using a shovel. When the incubator was mostly exposed, I slipped a bag over the incubator and sealed it with my hands to prevent the loss of fine sediment from within the incubator when it was pulled from the gravel. Once an incubator was removed, I counted the number of hatched alevins and retained the gravel for later processing. The gravel from each incubator was transported back to the laboratory and placed in a drying oven at 70°C until all moisture was removed. The gravel sample was then sifted through a series of progressively smaller sieves: 31.5 mm, 16 mm, 8 mm, 4 mm, 2 mm, 1 mm, 0.5 mm, and 0.125 mm. The mass of gravel retained by each sieve (gravel size class) was measured to the nearest 0.01 kg. The gravel composition was quantified as the proportion of the total sample mass represented by each gravel size class.

*Environmental Monitoring*

While monitoring water temperatures, I also collected river flow and water chemistry data at each incubator site on a weekly basis using a FlowTracker Handheld ADV and YSI probe, respectively. The YSI probe measured water temperature (°C), dissolved oxygen (mg/L), pH, and conductivity (mS/cm). Water chemistry measurements were taken just above the surface of the stream gravel. Water chemistry and river flow

were not monitored for several weeks in January because of thick ice cover on all the study sites.

*Statistical Analysis*

All statistical analyses were conducted using the R Statistical Computing Environment (version: 3.2.4; R Core Team, 2015). Egg mass was compared among the populations using an ANCOVA with female length as a covariate and population as a fixed effect. Hatch success was calculated as the number of individuals that successfully hatched relative to the total number of live embryos at the eyed-up stage. I compared in-situ hatch success among populations using a logistic regression with population as a fixed effect, and site, sire and dam as random effects. The significance of the population fixed effect ($\alpha = 0.05$) was tested using a Wald $\chi^2$ test (Bolker et al., 2009). We also compared the environmental variables measured in each river during the experiment using a linear mixed model with population as a fixed effect and site as a random effect.

Within each population, I used a logistic regression analysis and forward step-wise model selection procedure to assess the influence of site, egg mass, growing degree days, and the incubator gravel composition on in-situ hatching success (Bolker, 2008). Growing degree days was calculated for each family as the cumulative sum of mean daily temperature experienced between fertilization and incubator removal (Jensen et al., 2008). Gravel composition was included in the models as the first three axes from population specific principal component analyses (PCA) of incubator gravel composition (Appendix C.1-C.3). The first three PCA axes had eigenvalues greater than one and explained a significant amount of the variation in gravel composition (Tabachnick & Fidell, 2007). Because I was specifically interested in egg mass, the forward step-wise model selection procedure started with a base model including egg mass as a covariate, and sire and dam as random effects. I then tested for the inclusion of site, degree days, gravel composition PCA axes, a quadratic egg mass term, and all two-way interactions between egg mass and gravel composition. All covariates were standardized to a mean of zero and a standard deviation of one. All terms found to be significant using a Wald $\chi^2$ test were retained in the models during the selection procedure (Bolker et al., 2009; Zuur,

Ieno, Walker, Saveliev, & Smith, 2009). For the selected models, I estimated the variation explained by the fixed effects (marginal $R^2$) and full model (conditional $R^2$) using the approach of Nakagawa and Schielzeth (2013). A "global" egg mass model was also fit by combining the hatching success data for all three populations and fitting a logistic regression model without population as a fixed effect using the same forward step-wise procedure described previously; however, I used PC axes from an additional PCA run on the combined gravel composition data and I did not include a site term in the model. The site term was excluded because it would function much like a population fixed effect and we were interested in determining if there is a general egg mass – survival trend that may be operating independently of population.

I used selection differentials and gradients to evaluate how selection acted on egg mass in-situ. Selection differentials were calculated as the weighted mean egg mass after in-situ rearing minus the weighted mean egg mass before in-situ rearing for each population. Egg mass was weighted by the number of living individuals from each family. A linear regression between relative fitness (i.e., relative in-situ survival) and egg mass was used to estimate linear and quadratic egg mass selection gradients in each population (Lande & Arnold, 1983). Quadratic selection gradients were corrected by multiplying the quadratic term and its standard error by two (Lande & Arnold, 1983). I used a linear regression approach instead of transforming logistic regression coefficients following Janzen and Stern (1998) because the latter approach only applies to linear selection gradients. I also provide variance standardized selection differentials and gradients (Lande & Arnold, 1983).

I compared hatch success in the hatchery among populations using a logistic regression with population as a fixed effect, and sire and dam as random effects. To assess egg mass effects within populations, we used logistic regression analysis and a similar forward-step wise model selection procedure as described above; however, we only tested for the addition of a quadratic egg mass term. Additionally, a Spearman correlation analysis was used to assess whether families that performed well in the hatchery performed comparatively well in the wild based on the proportion of surviving

alevins in each rearing environment. The correlation analysis was run for each population separately.

*Population-Level Consequences*

I used a simulation analysis to determine the extent to which changes in female body size would scale up to affect alevin production in the river systems. Since egg mass is positively related to female length, one of the most plausible ways in which egg mass may change within a population is through interannual variation in female length (Braun, Patterson, & Reynolds, 2013). Female length fluctuates from year-to-year within a population due to a variety of factors, such as density dependent effects (Lorenzen & Enberg, 2002) or changes in prey resources (Jacobson, Gårdmark, Östergren, Casini, & Huss, 2018; Jones, 1986), and such variation is known to occur in Great Lakes Chinook salmon populations (Johnson & Gonder, 2013; Ontario Ministry of Natural Resources and Forestry, 2017).

For the analysis, I simulated a hypothetical population of female salmon based on the Credit River and Sydenham River using five different female length scenarios (expressed relative to current female length): 10% reduction in female length, 5% reduction in female length, current female length, 5% increase in female length, and 10% increase in length. The Credit and Sydenham Rivers were selected for the simulation because the egg mass selection gradients from these systems represent quadratic and directional selection gradients, respectively. The female length scenarios are within the known range of female length variation for Great Lakes Chinook salmon populations (Johnson and Gonder, 2013; OMNRF, 2017). The 10% increase in female length scenario was not applied to the Credit River because the length of females in 2012 was near the upper range of the population. The simulation analysis proceeded using the following steps for each female length scenario/population combination (Figure 4.3):

1. Generate a female length for 5000 virtual females by randomly sampling from a normal distribution with a mean female length equal to the scenario of interest. Standard deviation in female length was held constant among the scenarios and was equal to that measured in the current study.

2. Apply population specific female length – egg mass relationships to generate an egg mass for each simulated female. These relationships were derived from a linear regression run on female length and egg mass data collected during this study. Add a random deviation to each prediction that is drawn from a normal distribution with a mean of zero and a standard deviation equal to the standard deviation of model residuals.

3. Use a female length – fecundity relationship to derive a fecundity estimate for each female. Most salmon populations have a positive relationship between female length and fecundity (Einum, Kinnison, & Hendry, 2004), including the Sydenham River population. I estimated fecundity for each simulated female using a linear model fit to Sydenham River female length and fecundity data collected by Gerson et al. (2016) in 2010 and 2011 (fecundity = 13.906*female fork length – 4802.239). I added random deviations to the fecundity predictions by drawing from a normal distribution with a mean of zero and a standard deviation of 1267.4. I did not use my own population specific relationship because our scientific collectors permit did not allow me to euthanize salmon for the collection of gametes and, therefore, we could not determine fecundity for any of our fish.

4. Use the population specific egg mass selection gradient to predict the proportion of eggs that will hatch for each simulated female. Add a random deviation to the prediction that is drawn from a normal distribution with a mean of zero and a standard deviation equivalent to the prediction error.

5. Combine the simulated fecundity and hatching probability for each female to predict the number of alevins produced by the female. Sum the number of alevins produced per female to get the number of successfully hatched alevins in the population.

6. Repeat the simulation 10000 times for each egg mass scenario to derive the distribution of alevin production.

The simulation is not meant to be predictive of alevin production in the wild, but instead demonstrate the relative effect of egg mass on the production of alevins along an egg mass selection gradient. Therefore, I compared alevin production from the various

female length scenarios relative to the current female length scenario in each population. I also ran the simulation without the female length – fecundity relationship (i.e. random variation in fecundity) to understand how fecundity may interact with egg mass to influence alevin production.

## 4.3 Results

*In-Situ Rearing and Survival*

Eyed-up families were transferred to the rivers between 17 October 2012 and 8 November 2012. A total of 12 Credit River, 21 Pine River, and 20 Sydenham River families were successfully transferred (Table 4.1). Limited suitable spawning habitat at the Credit River study area prevented me from transferring all 20 Credit River families that were fertilized in the hatchery. The egg mass of transferred families was greater in the Credit (mean ± SE: 0.28 ± 0.02 g) and Sydenham Rivers (0.21 ± 0.01 g) than the Pine River (0.18 ± 0.01 g; population: $F_{2,49} = 7.99$, $P = 0.001$). While rearing, the populations experienced a decline in temperature from a high of 11°C at the time of installation to a low of ~ 0 °C (Table 4.1). Most of the environmental variables varied among the populations, except for the mean hyporheic temperature (Table 4.1). Survival in-situ varied across the populations with the Credit River having a lower survival (mean ± SE: 9 ± 3%) than both the Pine River (38 ± 7%) and Sydenham River (41 ± 5%; Population: $\chi_2^2 = 17.12$, $P < 0.001$).

Within populations, egg mass had a variable effect on in-situ survival. In the Credit River, egg mass had a non-linear, quadratic relationship with in-situ survival, whereby the highest survival was at an intermediate egg mass and the lowest survival was at the egg mass extremes (Table 4.2; Figure 4.4a). In-situ survival in the Pine River was positively related to the growing degree days experienced by a family, whereas survival was not related to egg mass (Table 4.2; Figure 4.4c). Egg mass had a positive, linear relationship with in-situ survival in the Sydenham River, whereby large eggs experienced higher in-situ survival (Table 4.2; Figure 4.4e). The models explained between 20% and 52% of the variance in survival with egg mass and parental effects explaining approximately equal proportions of the variance (Table 4.2). Neither site or gravel

composition PC axes were found to have significant effects on in-situ survival within the populations ($P > 0.05$). Furthermore, there were no two-way interactions between the gravel PC axes and egg mass ($P > 0.05$). When the population data was combined into a global model, egg mass had a quadratic relationship with in-situ survival (Egg Mass$^2$: -0.33 ± 0.16, Z = -2.03, P = 0.04). Furthermore, in-situ survival was negatively related to the gravel composition PC1 scores (PC1: -0.63 ± 0.26, Z = -2.45, P = 0.01; Figure 4.5). The PC1 axis had a strong negative loading for medium gravel size and strong positive loadings for sediment size classes < 4 mm (Appendix C.4), which indicates that survival was higher in substrate with larger gravel and low sand content. There was a gradient in gravel composition among the populations with the Sydenham River having the most preferable gravel composition, followed by the Pine River, and the Credit River had the poorest gravel composition (Figure 4.5).

Selection differentials and gradients for egg mass were consistent with the results from the logistic regression analyses (Table 4.3). In the Credit River, the greatest number of surviving individuals hatched from eggs close to the population mean and, as a result, the egg mass selection differential was small and not significantly different than zero (Table 4.3). Egg mass had a strong quadratic relationship with relative fitness in the Credit River (Table 4.3). The Pine River egg mass selection differential and gradient were both found not to be different than zero (Table 4.3). The egg mass selection differential in the Sydenham River was positive and significantly greater than zero indicating that the mean egg size of the population has increased after the selection event (Table 4.3). This finding is further supported by the positive, linear selection gradient in the Sydenham River (Table 4.3).

*Hatchery Survival*

Hatchery survival was very high for all populations and there were no significant differences in survival among the populations (Credit: 96 ± 1%; Pine: 99 ± 1%; Sydenham: 99 ± 1%; Population: $\chi_2^2$ = 3.87, P = 0.14). Egg mass did not influence hatchery survival for the Credit River (Table 4.2; Figure 4.4b). In contrast, there was a weak, linear relationship between egg mass and hatchery survival for both the Pine and

Sydenham Rivers (Table 4.2; Figure 4.2d and 4.2f). The models explained between 20% and 55% of the variation in hatchery survival with parental effects explaining less than half to almost all the variation (Table 4.2). Interestingly, the performance of a family in the hatchery (i.e., survival rate) was not an indicator of its performance when reared in-situ for any of the populations (Credit River: $\rho = -0.18$, $P = 0.57$; Pine River: $\rho = 0.14$, $P = 0.55$; Sydenham River: $\rho = 0.23$, $P = 0.34$).

*Population-Level Consequences*

The simulation analysis showed that the population-level consequences of changing female length can be substantial (Figure 4.6); however, the effects were sensitive to the shape of the in-situ egg mass selection gradient and its interaction with fecundity. For the simulations that did not have a female length-fecundity relationship, the relative production of alevins followed a predictable pattern and closely aligned with the egg mass selection gradients for the Credit (quadratic) and Sydenham Rivers (linear; Figure 4.6). The presence of a female length-fecundity relationship in the simulation changed the relative production of alevins among the female length scenarios for both populations. The decreased female length scenarios showed a greater reduction in alevin production, while the increased female length scenarios showed an elevated alevin production relative to the simulations without a female length-fecundity relationship (Figure 4.6). In the case of the Credit River, the greater fecundity with a 5% increase in female length was enough to offset the decreased survival associated the higher egg mass.

**Table 4.1:** Date the first incubator was installed, date the last incubator was removed, number of incubator sites, length of river between the upstream site and downstream site, number of families planted, total number of eggs planted, developmental degree days, surface environmental conditions, and hyporheic environmental conditions in each river. Temperature was measured continuously at hourly intervals using HOBO temperature loggers placed at the gravel surface and within a planted incubator at each incubator site. Flow and water chemistry were measured weekly at each incubator site using a FlowTacker and YSI probe, respectively. The gravel composition within each incubator (median and % fines) was measured at the cessation of the study. Degree days and all environmental variables are reported as mean (minimum – maximum). Environmental variables were compared using a linear mixed model with population as a fixed effect and site as a random effect. Different superscript letters indicate population differences.

| | **Credit River** | **Pine River** | **Sydenham River** |
|---|---|---|---|
| Date Installed | 8/11/2012 | 17/10/2012 | 19/10/2012 |
| Date Removed | 7/02/2013 | 17/01/2013 | 08/02/2013 |
| # Incubator Sites | 2 | 3 | 3 |
| Reach Length (m) | 310 | 260 | 230 |
| # Families | 12 | 21 | 20 |
| # Eggs Planted | 1104 | 1918 | 1988 |
| Degree Days | 535.2 (530 - 541)$^{a}$ | 553.0 (520 - 593)$^{a}$ | 492.0 (466 - 568)$^{a}$ |
| *Surface Environment* | | | |
| Flow ($m \cdot s^{-1}$) | 0.32 (0.12 – 0.60)$^{a}$ | 0.77 (0.48 – 1.0)$^{b}$ | 0.49 (0.36 – 0.76)$^{ab}$ |
| Temperature (°C) | 1.92 (-0.13 – 8.63)$^{a}$ | 3.65 (-0.02 – 11.07)$^{b}$ | 2.04 (-0.80 – 8.52)$^{a}$ |
| Dissolved Oxygen ($mg \cdot L^{-1}$) | 13.2 (12.1 – 14.4)$^{a}$ | 12.5 (10.4 – 14.4)$^{b}$ | 12.8 (10.6 – 14.1)$^{ab}$ |
| pH | 8.3 (7.8 – 8.7)$^{a}$ | 8.3 (7.8 – 8.5)$^{a}$ | 8.2 (7.8 – 8.5)$^{a}$ |
| Conductivity ($ms \cdot cm^{-1}$) | 0.80 (0.74 – 0.94)$^{a}$ | 0.52 (0.40 – 0.53)$^{b}$ | 0.49 (0.41 – 0.54)$^{b}$ |
| *Hyporheic Environment* | | | |
| Median Gravel Size (mm) | 14.9 (11.8 – 24.3)$^{a}$ | 19.9 (12.7 – 26.4)$^{ab}$ | 23.6 (19.3 – 28.6)$^{b}$ |
| % fine sediment (< 4mm) | 14 (6 – 18)$^{a}$ | 9 (3 – 19)$^{ab}$ | 2 (1 – 7)$^{b}$ |
| Temperature (°C) | 2.04 (-0.03 – 8.65)$^{a}$ | 3.89 (0.16 – 10.90)$^{a}$ | 3.10 (0.02 – 11.96)$^{a}$ |

**Table 4.2:** Parameter estimates, test statistics, p-values, marginal $R^2$ and conditional $R^2$ from Credit River, Pine River, and Sydenham River logistic regression models fit separately to in-situ and hatchery survival data. Bolded estimates are significant ($P < 0.05$). Standard errors associated with the sire and dam random effects were estimated by bootstrapping for 1000 iterations. Egg mass covariates were retained in all models, regardless of significance. Z-statistics are provided for model covariates and $\chi^2$-statistics from likelihood ratio tests are provided for random effects.

| Habitat | Population | Parameter | Estimate (± SE) | Z- or $\chi^2$-statistic | P-value | Marginal $R^2$ | Conditional $R^2$ |
|---|---|---|---|---|---|---|---|
| In-situ | Credit | **Intercept** | **-1.82 (0.77)** | **-2.35** | **0.018** | 0.26 | 0.52 |
| | | Egg Mass | 0.39 (0.58) | 0.68 | 0.500 | | |
| | | **(Egg Mass)$^2$** | **-1.55 (0.59)** | **-2.63** | **0.008** | | |
| | | **Sire** | **2.37 (0.88)** | **3.91** | **0.048** | | |
| | | Dam | 0.00 (0.34) | 0.00 | 1.0 | | |
| | Pine | **Intercept** | **-0.96 (0.36)** | **-2.66** | **0.008** | 0.18 | 0.48 |
| | | Egg Mass | 0.46 (0.36) | 1.28 | 0.200 | | |
| | | **Degree Days** | **1.07 (0.37)** | **2.87** | **0.004** | | |
| | | Sire | 0.00 (0.00) | 0.00 | 1.0 | | |
| | | **Dam** | **2.54 (0.37)** | **171.17** | **<0.001** | | |
| | Sydenham | **Intercept** | **-0.43 (0.19)** | **-2.31** | **0.021** | 0.08 | 0.20 |
| | | **Egg Mass** | **0.67 (0.19)** | **3.56** | **<0.001** | | |
| | | Sire | 0.00 (0.00) | 0.00 | 1.0 | | |
| | | **Dam** | **0.64 (0.10)** | **151.6** | **<0.001** | | |
| Hatchery | Credit | **Intercept** | **3.83 (0.43)** | **8.93** | **< 0.001** | 0.001 | 0.20 |
| | | Egg Mass | -0.09 (0.37) | -0.24 | 0.811 | | |
| | | Sire | 0.00 (0.03) | 0.00 | 1.0 | | |
| | | **Dam** | **1.08 (1.78)** | **8.61** | **0.003** | | |
| | Pine | **Intercept** | **4.94 (0.42)** | **11.81** | **< 0.001** | 0.14 | 0.20 |
| | | **Egg Mass** | **0.86 (0.26)** | **3.32** | **<0.001** | | |
| | | Sire | 0.09 (0.71) | 0.02 | 0.88 | | |
| | | Dam | 0.22 (1.90) | 0.10 | 0.75 | | |
| | Sydenham | **Intercept** | **5.94 (1.05)** | **5.68** | **<0.001** | 0.23 | 0.55 |
| | | **Egg Mass** | **1.47 (0.70)** | **2.10** | **0.035** | | |
| | | Sire | 1.99 (2.20) | 0.12 | 0.73 | | |
| | | Dam | 1.06 (3.71) | 1.31 | 0.25 | | |

**Table 4.3:** Egg mass selection differentials (95% CI), linear selection gradients (β; SE), and quadratic selection gradients (γ; SE) for the Credit, Pine, and Sydenham Rivers when reared in-situ. Selection differentials and gradients are presented as raw and variance standardized (STD). Selection gradients were estimated using a linear regression between relative fitness and egg mass. The Pine River linear regressions also included degree days as a covariate. Selection differential confidence intervals were estimated using a bootstrap procedure run for 1000 iterations. Bolded selection differentials and gradients are greater than zero.

| Population | Data Type | Selection Differential | β | γ |
|---|---|---|---|---|
| Credit R. | Raw | 0.005 (-0.02, 0.03) | 1.32 (6.82) | **-605.75 (231.37)** |
| | STD | 0.10 (-0.43, 0.61,) | 0.07 (0.36) | **-1.68 (0.64)** |
| Pine R. | Raw | 0.006 (-0.005, 0.02,) | 3.92 (4.56) | -71.34 (204.42) |
| | STD | 0.18 (-0.19, 0.46,) | 0.13 (0.15) | -0.08 (0.23) |
| Sydenham R. | Raw | **0.012 (0.004, 0.02)** | **8.85 (2.80)** | -114.87 (132.48) |
| | STD | **0.32 (0.12, 0.50)** | **0.33 (0.11)** | -0.16 (0.19) |

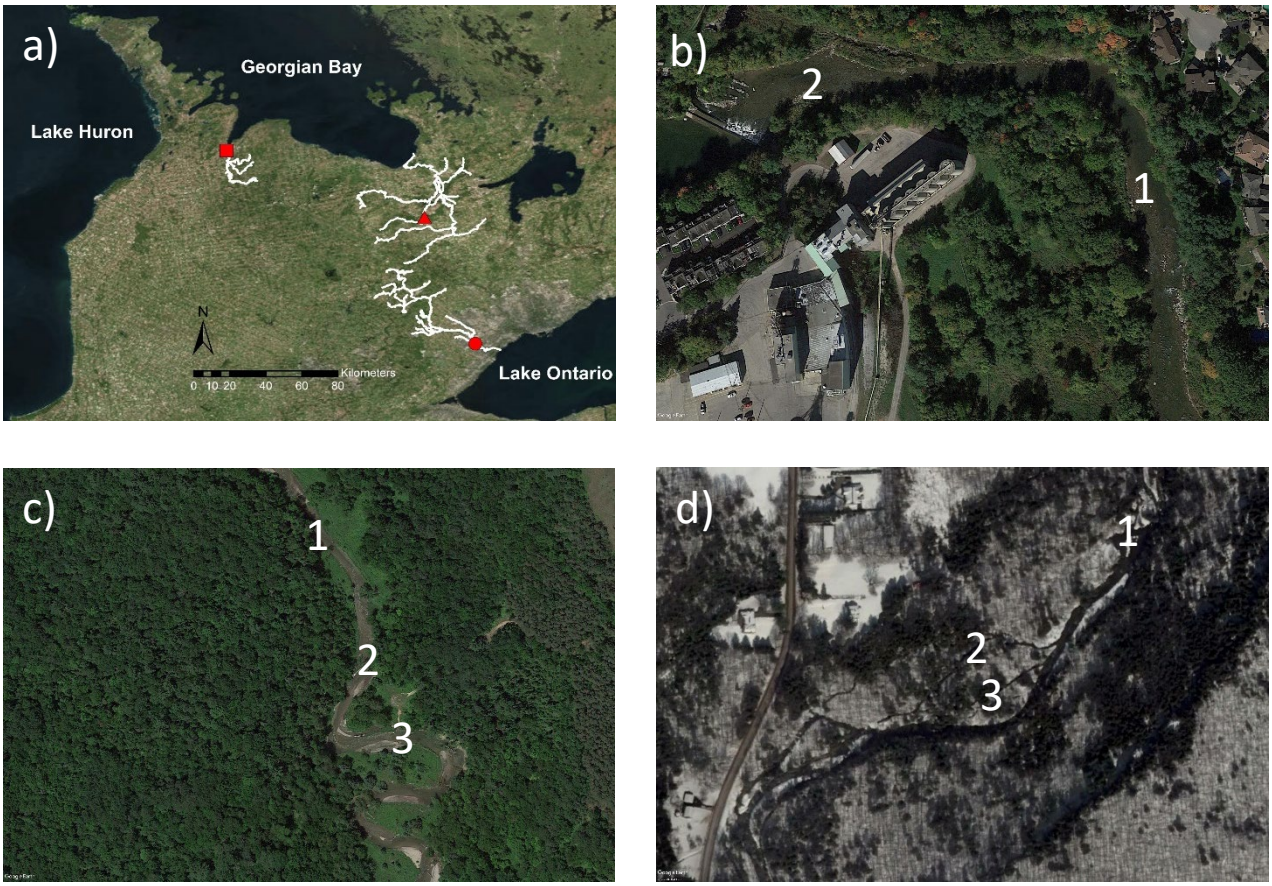


**Figure 4.1:** Map showing the study site locations in Ontario, Canada (a; circle = Credit, triangle = Pine, and square = Sydenham) along with more detailed satellite images of the (b) Credit River, (c) Pine River, and (d) Sydenham River. Within each river, there were 2-3 incubator sites (labelled 1-3) each containing 6-8 incubators. The incubator sites were placed in areas of known salmon spawning habitat. Satellite imagery was derived from ArcMap 10.3 (a; ESRI, 2015) and Google Earth 7.3.0 (b,c, and d; Google, 2018).

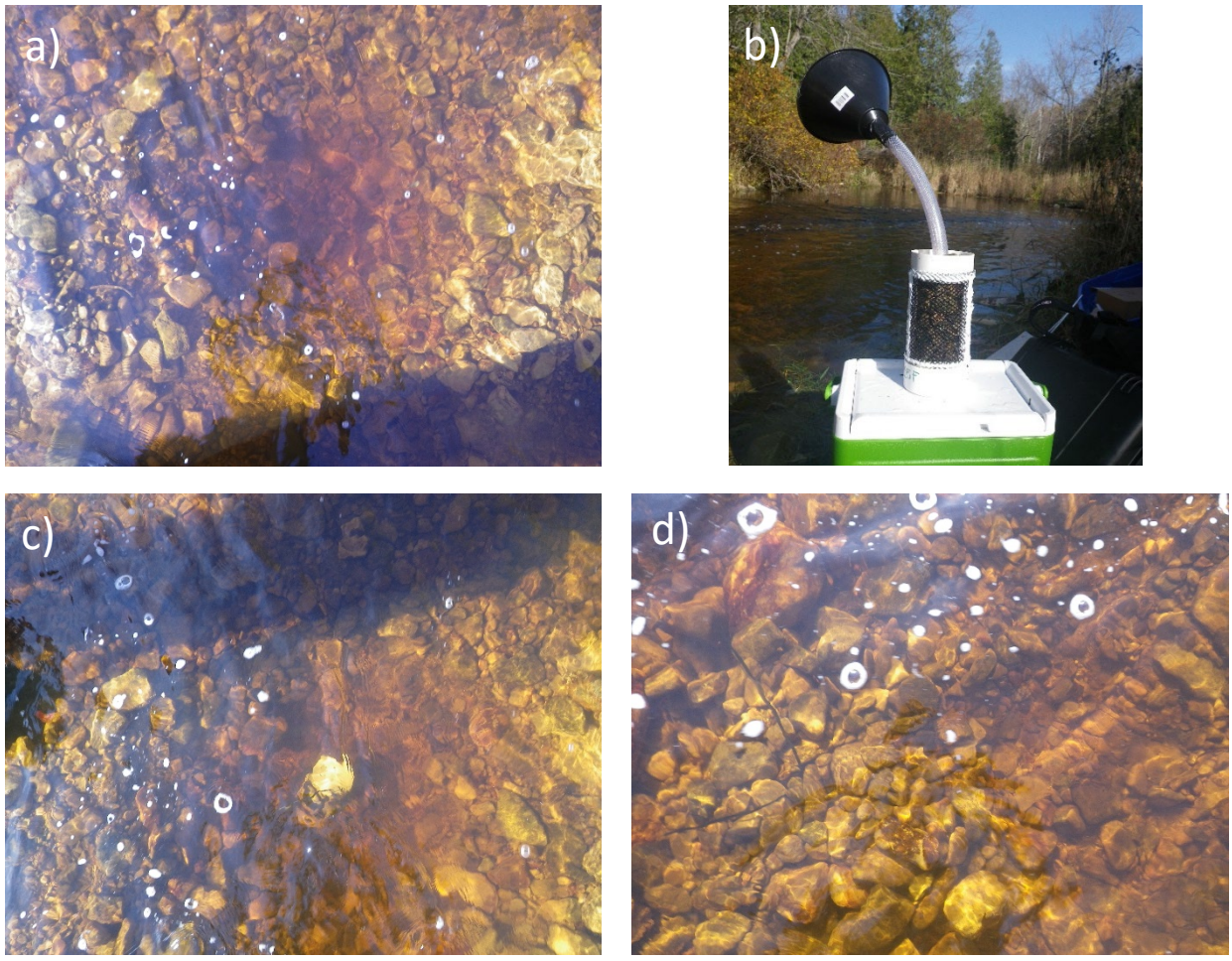


**Figure 4.2:** Steps in the incubator installation process: a) digging of the artificial redd; b) incubator with site specific gravel and egg installation tube; c) incubator placed in the artificial redd, and d) completed artificial redd with incubator installed. The river flows from right-to-left in the photographs. Notice the cable ties used to locate the incubator sticking out of the gravel of the completed artificial redd.

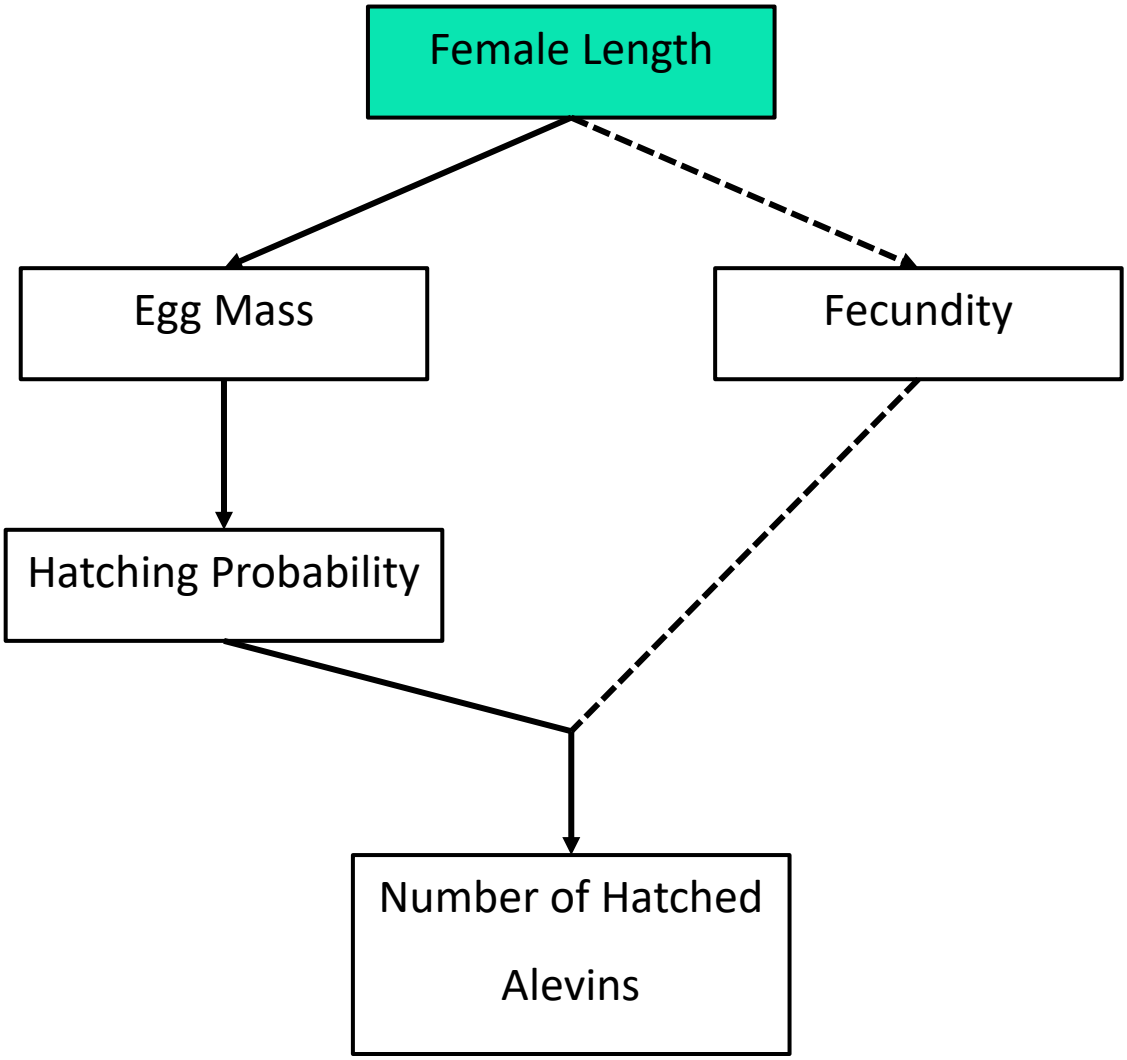


**Figure 4.3:** Schematic of the simulation analysis used to determine how changes in female length, and, in turn, egg mass will affect the number of alevins produced in each Chinook salmon population. Solid arrows point to data derived from empirical relationships estimated using data in the current study and dashed arrows indicate data derived from published relationships. Lines that connect represent data that was multiplied. Each egg mass scenario was run for 10000 iterations and each iteration consisted of a hypothetical population of 5000 females. The green box indicates the beginning of the simulation analysis pathway.

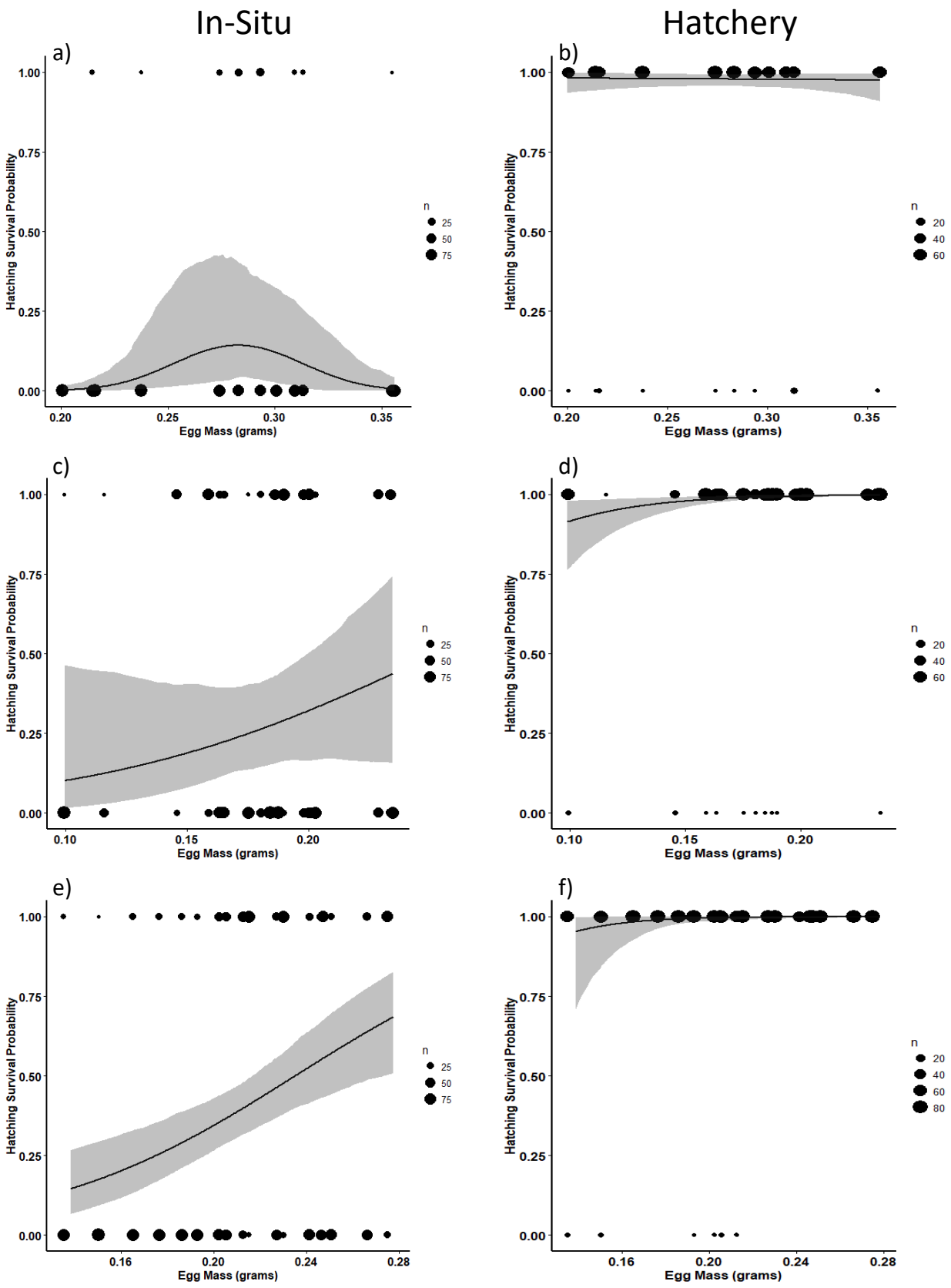


**Figure 4.4:** Hatching survival probability versus egg mass for the (a,b) Credit River, (c,d) Pine River, and (e,f) Sydenham Rivers when reared in-situ and in the hatchery. Point size is proportional to the number of individuals alive or dead for each egg mass. Bootstrap 95% confidence intervals are represented by the grey shaded bands.

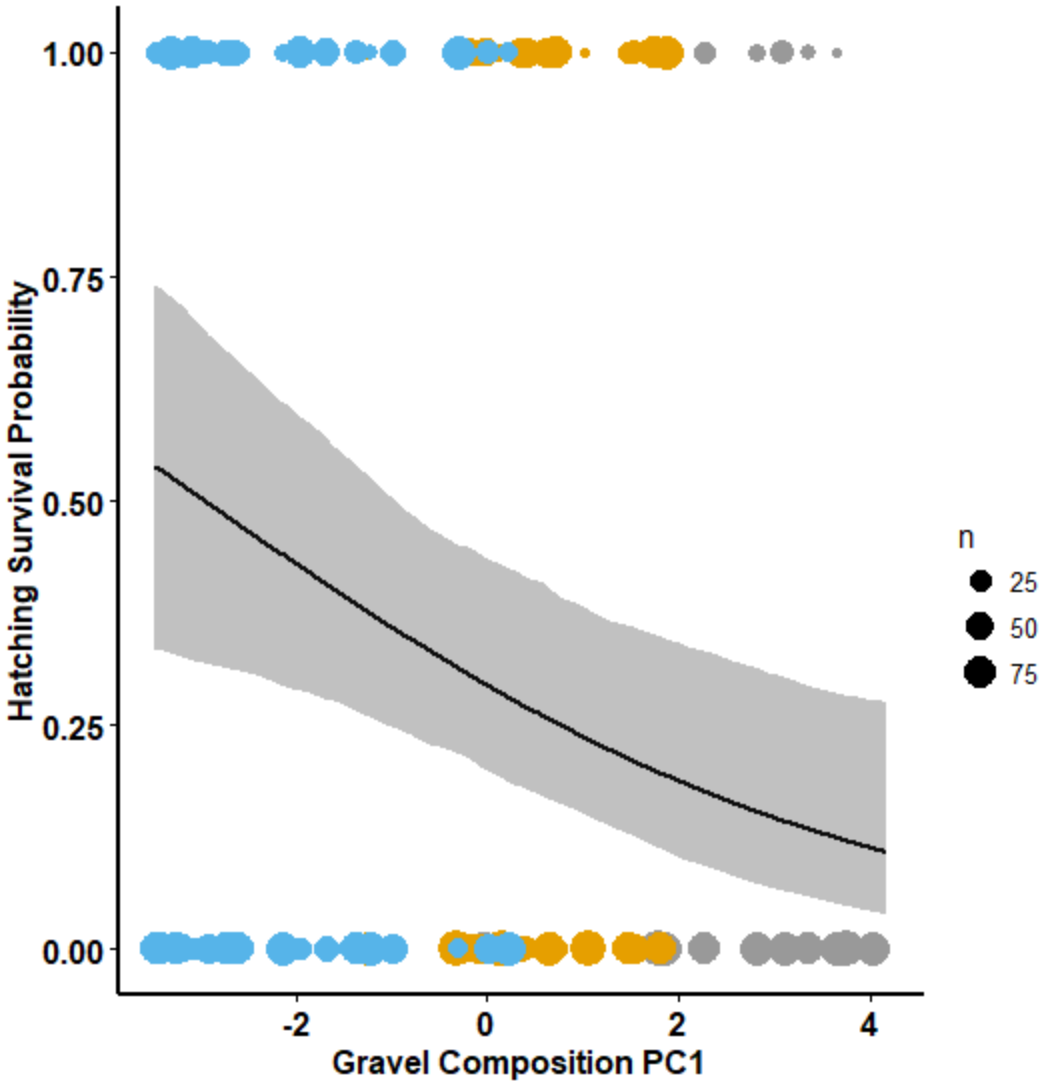


**Figure 4.5:** Hatching survival probability versus gravel composition PC1 from a logistic regression fit to data from the Credit (grey), Pine (orange), and Sydenham Rivers (blue). The relationship is plotted while holding egg mass constant at the mean for the data set.

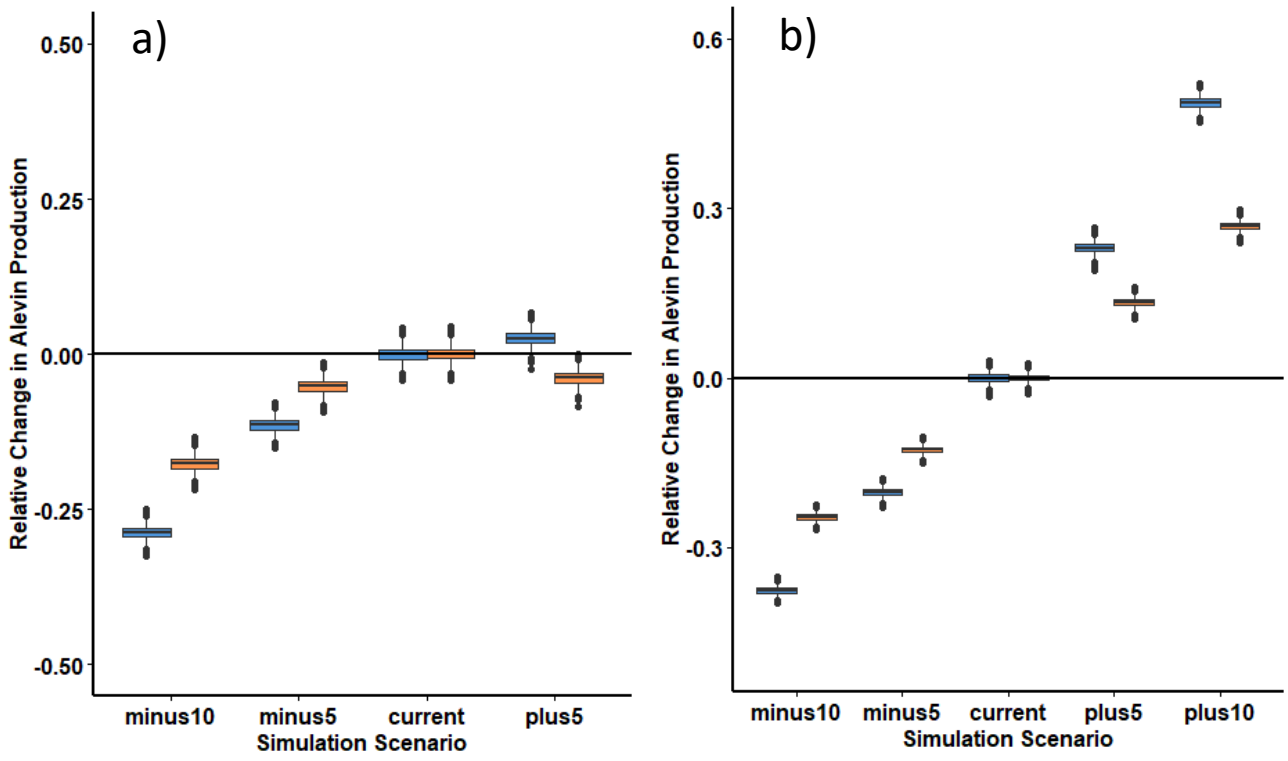


**Figure 4.6:** Relative change in the number of alevins produced by the (a) Credit River and (b) Sydenham River under several different egg mass scenarios: 10% reduction in female length (minus10), 5% reduction in female length (minus5), current egg mass (current), 5% increase in female length (plus5), and a 10% increase in female length (plus10). Results are presented for simulations with (blue) and without (orange) a positive female length-fecundity relationship. The scenarios are compared relative to the median alevin production in the current scenario (solid line). The plus10 scenario was not run for the Credit River because this would have resulted in a female length outside of the historical range of female lengths in this population. The number of alevins produced was simulated using a hypothetical population of 5000 females, population specific egg mass – hatching success and egg mass – female length relationships, and previously published female length – fecundity relationships. Each simulated scenario was run for 10000 iterations. See main text for a detailed explanation of the simulation analysis.

## 4.4 Discussion

I reared embryos from three Great Lakes Chinook salmon populations in the wild and showed that egg mass can have a strong effect on in-situ survival. The shape of the egg mass – survival relationship was different among the populations and included both linear and non-linear responses. Variation in gravel composition did not influence in-situ survival within the populations, but it did have strong effects when evaluated across the populations. Interestingly, hatchery rearing did not provide reliable information on the strength/shape of the egg mass-survival relationships nor did the performance of a family in the hatchery correlate with its performance in the wild. When I applied the observed in-situ egg mass-survival relationships in a simulation model, I found that egg mass effects could greatly influence alevin production at the population-level.

*In-Situ Rearing and Survival*

In-situ survival from eyed-up to hatching averaged between 9% and 41% among my study populations, which is equal to or less than survival estimates from other systems (Johnson et al., 2012; Merz, Setka, Pasternack, & Wheaton, 2004; Roni et al., 2016; Stark et al., 2018). For example, Merz et al. (2004) reared Chinook salmon in-situ from eyed-up to emergence in the Mokelumne River, California and observed mean survival rates between 22% and 61%. Direct comparison of survival rates from our study to those in other systems is difficult because most studies of Chinook salmon in-situ survival have quantified survival from fertilization/eyed-up to emergence. Therefore, my survival estimates should be viewed as optimistic relative to those published in other studies. Survival estimates from our study suggest that significant mortality can occur between eyed-up and emergence and that the period up to hatching represents an important selection event. There is a possibility that the incubators we used contributed to the low survival we observed in our study systems; however, my incubator used a similar mesh size and was of a volume equal to or greater than other studies, which makes increased mortality rates due to the incubator unlikely.

Egg mass had a significant effect on in-situ survival in two of the three populations. In the Sydenham River, there was strong directional selection for larger egg

mass. This observation that “bigger is better” during early life is consistent with previous studies on salmonids (Einum & Fleming, 2000; Robertsen, Skoglund, & Einum, 2013) and other teleost fishes (Sogard, 1997). However, the stabilizing selection gradient for egg mass observed in the Credit River indicates that we cannot assume larger eggs will perform better within a population. Stabilizing selection has rarely been observed during the early life of salmon, with the only observations being for length in 1+ and 2+ Atlantic salmon (*Salmo salar*; Hendry, Letcher, & Gries, 2003). It is evident that bigger is not always better and researchers should be weary of making such an assumption.

A large proportion of the variation in in-situ survival was explained by parental effects. More specifically, maternal effects had a strong influence on in-situ survival, whereas genetic effects (i.e., sire effects) were relatively weak. Sire effects appeared to be strong in the Credit River population, but the variance component estimates from this population must be viewed carefully due its low sample size and an unbalanced mating design. Roni et al. (2016) found that family identity had a significant effect on the in-situ survival of Chinook salmon from fertilization to emergence; however, the researchers were unable to partition the parental effects into sire and dam components. The results of our study are consistent with those from hatchery-based studies that have shown maternal effects to be strong between fertilization and emergence (Evans, Neff, & Heath, 2010; Houde et al., 2013; Thorn & Morbey, 2018). Genetic effects are expected to become increasingly important as fish progress through ontogeny (Heath et al., 1999; Wilson, Kruuk, & Coltman, 2005). For example, Serbezov et al. (2010) was able to partition the variation in length-at-age for brown trout in a natural stream and found that genetic effects were stronger than maternal effects for later developmental stages (i.e., juvenile - adult). Therefore, it is important to consider the developmental stage when trying to understand the factors influencing survival within a population and that maternal effects are likely to predominate prior to emergence.

Survival was highest in the Pine and Sydenham Rivers and lowest in the Credit River population. The pattern of survival among the populations matched that of spawning substrate fine sediment content (< 4mm), whereby the Credit River had the lowest survival and highest fine sediment content. Previous studies have found that there

is a negative relationship between fine sediment content and embryo survival in salmonids (reviewed by Chapman 1988, Jensen et al. 2009). Fine sediment reduces substrate permeability and the intragravel flow of water within the redd, which can lead to the creation of hypoxic conditions within the egg pocket (Chapman, 1988; Greig, Sear, & Carling, 2005). Furthermore, the fine sediment can seal the surface of the redd and prevent the escape of emerging juveniles (Fudge, Wautier, Evans, & Palace, 2008). The effects of fine sediment can be mitigated by high tributary flows that help to aerate the hyporheic environment and/or remove fine sediment from the redd (Greig et al., 2007). Surficial flow velocity was lowest in the Credit River and this likely exacerbated the effects of the fine sediment that had accumulated in the artificial redds during the study.

Gravel composition did not affect in-situ survival within the populations; however, the gravel composition did influence survival when all the population data were combined, indicating that variation in gravel composition was operating at a larger spatial scale than the individual study reaches within each river. Riverine habitat varies at different spatiotemporal scales depending on the environmental variable of interest (Frissell, Liss, Warren, & Hurley, 1986; Wiens, 2002). It is likely that the gravel composition within our study reaches lacked variability because our study reaches were short in length (230 – 310 meters). Studies of salmonid in-situ survival that have found no relationship between redd environmental characteristics and survival (e.g., Gauthey et al., 2017) could be operating at too narrow a spatial scale for the environmental variable of interest. When designing in-situ studies, therefore, researchers should be cognizant of the spatial scale at which environmental variables operate within a riverine system.

*Hatchery Survival*

Population- and family-level survival in the hatchery provided a poor proxy for survival in the wild. Survival rates for the populations in the hatchery were drastically different than those in the wild, and family-level survival did not correlate between hatchery and in-situ environments for any population. The shape of the egg mass – survival relationship for the Credit River and Pine River was different between the hatchery and wild, whereas the strength of egg mass – survival relationship was different

between the environments for the Sydenham River. Furthermore, the variance explained by the parental effects also differed between the rearing environments. The lack of congruence between the hatchery and in-situ results emphasizes the need to assess a population's performance in the wild and to refrain from making extrapolations from hatchery-based studies to natural conditions.

*Population-Level Consequences*

The relative position of a population along an egg mass selection gradient can have population-level effects on the number of alevins produced. Whether more or less alevins are produced in a given year will depend on the match between female reproductive investment (i.e., egg mass) and the incubation selection environment. Though our simulation is simplistic, our results are consistent with a growing body of research that has found a link between maternal condition or investment and production in fish populations (Marshall & Frank, 1999; Marshall, Yaragina, Lambert, & Kjesbu, 1999; Vallin & Nissling, 2000; Venturelli, Shuter, & Murphy, 2009; Venturelli et al., 2010). For example, Venturelli et al. (2010) used a field experiment and population modelling to show that female age structure, along with its positive relationship with egg size, can have a significant effect on the population dynamics of an exploited walleye (*Sander vitreus*) population. Overall, our results suggest that the interaction between maternal reproductive investment and early life history survival is an important factor contributing to the production of fish populations.

*Conclusion*

I have shown that the survival of Chinook salmon from eyed-up to hatching in the wild is strongly influenced by egg mass within populations, and that the shape of the egg mass – survival relationship is different among populations. Survival in the wild was further influenced by the gravel composition of the redd environment, where sandy substrates were associated with poor survival. Interestingly, the egg mass – survival relationships observed in the paired hatchery study were not transferrable to the wild. Using simulation, we found that the effect of egg mass on survival was apparent at the population-level through variation in alevin production. Our study monitored survival up

to the hatching stage and the effects of egg mass are known to extend well into the free feeding juvenile stage (Rollinson & Hutchings, 2013). Often, studies in the wild focus on a single developmental stage or a wide time period that integrates several developmental stages. Future studies should investigate the effects of egg mass on survival over all the major early life history developmental stages to better evaluate the population-level effects of the egg mass – survival relationship.

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# 5 General Conclusion

## 5.1 Summary of Findings

In this dissertation, I addressed three primary research questions related to the evolutionary ecology of maternal effects: 1) how do maternal effects contribute to the divergence of offspring phenotypes among populations (i.e., contemporary evolution)?; 2) how do transgenerational maternal effects influence offspring phenotypes across environmental conditions?; and 3) how do maternal effects influence offspring survival in the natural environment? In Chapter 2, I reared Chinook salmon embryos from three populations in a common garden hatchery study and found that egg size explained most of the within and among population variation in early life history traits, which suggests that egg size has the capacity to significantly influence the adaptive response of early life phenotypes. Because egg size is not the only maternal effect trait, I also assessed the effect of egg nutrient composition, which is a transgenerational maternal effect, on the expression of offspring phenotypes in Chapter 3 and determined that both the fatty acid and proximate composition of eggs influenced offspring phenotypes above and beyond the effect of egg size. Importantly, the effects of both egg size and nutrient composition were temperature dependent (Chapters 2 and 3). A primary concern for many studies of maternal effects is the lack of in-situ studies. In Chapter 3, I reared Chinook salmon embryos in-situ and found that egg size influences early life survival in various ways depending on the redd selection environment. Based on these in-situ egg size – survival relationships, I showed how variation in egg size could have population-level consequences for offspring production using a simulation model. I also reared embryos from the same families used in-situ within a hatchery and found that estimates of egg size and quantitative genetic parameters from hatchery-based studies should not be extrapolated to the wild. Here, I discuss the implications of my findings for the evolution of offspring traits and how they can inform the management of salmon populations.

## 5.2 Egg Quality and Evolution

### 5.2.1 Divergence

Egg size explained most of the within and among population variation in growth related early life history traits (Chapter 2 and 3). Previous studies on salmonids have shown that egg size can explain a significant proportion of the within population maternal effect (Haugen & Vøllestad, 2000) and that maternal identity is a primary contributor to population divergence (Aykanat, Bryden, & Heath, 2012). However, my work is the first to quantify the within and among population variation in offspring traits attributable to egg size, while also accounting for the breeding design. This is an important step forward because it demonstrates that egg size is the primary maternal effect trait influencing the within population variation in offspring traits, and that egg size has the capacity to affect both the magnitude and rate of phenotypic divergence among populations. Together, these results suggest that egg size is an important means through which offspring phenotypes may respond to new environments (or environmental change) in salmon. An important question that remains, however, is how much of the egg size effect is attributable to maternal genetic or environmental effects? Answering this question will require a multi-generational pedigree that is at least three generations deep (McAdam, Garant, & Wilson, 2014), but quantifying maternal genetic effects will provide information on how much of the egg size related variation in offspring traits is heritable (e.g., total heritability; Willham, 1972). Such knowledge will improve our ability to predict the evolution of offspring traits (McAdam & Boutin, 2004; McAdam, Boutin, Réale, & Berteaux, 2002).

Phenotypic differences among the introduced populations in my study remained after controlling for both egg size and egg nutrient composition (Chapter 2 and 3), which indicates that there are likely genetic differences among the populations for early life history traits. This is the first evidence that growth related early life history traits have genetically diverged among introduced Great Lakes Chinook salmon. The phenotypic divergence rates (0.007 to 0.36) for early life history traits among Great Lakes populations are consistent with those for other introduced salmonid populations (Haugen & Vøllestad, 2001; Hendry & Kinnison, 1999; Kinnison & Hendry, 2001). However, it is

still unclear whether this genetic divergence is due to natural selection, genetic drift, or founder effects. A reciprocal transplant experiment in which individuals from the three populations are raised in each tributary environment could identify whether natural selection played a part in the phenotypic divergence among the populations. More specifically, natural selection would be implicated if individuals reared in their home environment performed better (i.e., survive at higher rates) than individuals from a foreign environment (local vs. foreign criteria; Westley, Ward, & Fleming, 2012). Beyond identifying the signal of natural selection, it will not be possible to determine the relative contributions of natural selection, genetic drift and founder effects to the present population differences. A likely scenario, however, is that a mix of all three have acted to shape the current phenotypes in each population (Funk et al., 2016; Kolbe, Leal, Schoener, Spiller, & Losos, 2012; Runemark, Hansson, Pafilis, Valakos, & Svensson, 2010).

There was also evidence of metabolic divergence among the populations (Chapter 3). The egg fatty acid composition that produced the largest individuals (hatch and swim-up) was different among the Lake Huron populations (Pine and Sydenham River) and the Credit River population (Lake Ontario). Rarely has metabolic divergence been studied in the context of contemporary evolution in natural populations (but see Neely, Myers, Hard, & Shearer, 2008). Most often, studies of metabolic or digestive divergence have been conducted on populations that have been isolated for long periods of time (Sullam et al., 2015) or across closely related species (German et al., 2010; Wagner, McIntyre, Buels, Gilbert, & Michel, 2009). The evolutionary mechanism underlying the metabolic divergence among Great Lakes populations is still unknown and could be the result of phenotypic plasticity and/or genetic divergence. Gut morphology and digestive capabilities are known to be highly plastic and can change in response to fasting or changes in diet (German, Horn, & Gawlicka, 2004; Olsson, Quevedo, Colson, & Svanbäck, 2007; Zaldúa & Naya, 2014). Furthermore, genetic divergence could arise through selection acting directly on offspring metabolism or a correlated response to selection acting on adult metabolism. Further research is required to elucidate the evolutionary mechanism underlying the observed metabolic divergence. One way to investigate the metabolic divergence further is to run a three-generation common garden

study, whereby individuals from each generation/population are split into three feeding groups reflecting the diets of each study population. Such a design will allow for the variation in growth related traits to be partitioned between genetic and non-genetic sources (i.e., plastic effects).

### 5.2.2 Interactions with Offspring Environment

How egg size and nutrient content affected offspring phenotypes depended on temperature (Chapters 2 and 3). These maternally mediated plastic responses are important from an evolutionary perspective because they can affect the phenotypic variation available for selection. Both egg size and nutrients are shaped by the maternal rearing environment in salmon (Johnson, 2009; Jonsson & Jonsson, 2016; Jonsson, Jonsson, & Fleming, 1996; Wiegand, 1996) and, depending on the match between the maternal and offspring environment, the maternally mediated transgenerational effect could be adaptive or maladaptive (Marshall & Uller, 2007). For example, female seed beetles (*Stator limbatus*) produce larger, better provisioned eggs when exposed to a nutritionally poor host to prevent starvation related morality in their offspring; however, females raised on a high-quality host and switched to a low-quality host produced poorly provisioned eggs that led to low offspring survival (Fox, Thakar, & Mousseau, 1997). The survival benefit or cost associated with the transgenerational effects I observed remain unknown and a logical next step would be to assess when/where the transgenerational effects of egg size/nutrients are adaptive in the wild. This could be done by experimentally manipulating egg size/nutrients (e.g., Einum & Fleming, 1999) and raising the offspring under various natural conditions.

The temperature – egg quality interactions underlying offspring traits may have important implications within the context of climate change. Egg size had a positive relationship with all growth-related offspring traits and the strength of this relationship decreased with an increase in temperature. For egg nutrients, there was a positive relationship between egg lipid content and offspring growth, which increased in strength with an increase in temperature. A common thread linking these egg quality relationships is offspring metabolism. At high temperature, the metabolism of salmonids begins to decouple from offspring size (Régnier, Bolliet, Gaudin, & Labonne, 2013) and the energy

required for development increases due to a reduction in yolk conversion efficiency (Heming, 1982; Mueller et al., 2015). Given that climate change is expected to increase water temperatures, the effect of high temperature on salmonid metabolism has two implications for maternal effects. First, the ability of egg size to shape growth related offspring traits in a warming environment is reduced and, since additive genetic effects were low for most offspring traits at high temperature, salmon may have a limited ability to adapt. Second, the increased cost of development at high temperature for salmon means that female salmon will need to increase the energy they invest per offspring or risk producing offspring with reduced fitness (e.g., smaller size or poorly developed). Taken together, salmon may produce fewer offspring that are less able to adapt to a warmer environment. Whether such an outcome would occur in the wild is still unknown and more research is needed to understand the potential impacts of climate change on salmonids. A long-term observational study tracking water temperatures, the number of female spawners, their reproductive investment (egg size/number/nutrients), and the number of emerging juveniles or outmigrating smolts would provide the data needed to assess climate change impacts on reproductive investment and offspring survival in salmonids.

Whether an experiment is conducted in the hatchery or wild can significantly affect the estimation of egg size and parental effects (Chapter 4). For egg size specifically, the magnitude and/or the direction of the relationship with hatching success varied between the treatments in all three populations studied. My study is the first to conduct a paired hatchery-wild experiment using a within-family design to evaluate how hatchery derived observations transfer to the wild. The lack of agreement between hatchery and wild studies is important because researchers often use hatchery-based studies to understand how various biological/ecological processes affect fitness. My findings suggest that hatchery-based observations should be used with caution and that experiments should always be conducted in the wild when feasible.

### 5.2.3 In-situ Survival

In the wild, egg size and maternal effects had a significant effect on the hatching success of Chinook salmon (Chapter 4). The egg size selection gradients differed

between the populations with egg size having a concave (stabilizing selection), linear (directional selection), and no relationship with hatching success in the Credit, Sydenham, and Pine Rivers, respectively. These findings add to the few studies that have shown that egg size can affect hatching success in the wild (Einum & Fleming, 2000; Gauthey et al., 2017). Most studies of salmonid early life survival up to and including free feeding have found that "bigger is better" (Einum & Fleming, 2000; Robertsen, Skoglund, & Einum, 2013; Sogard, 1997). However, my study is the first to show that nonlinear selection gradients can occur during the hatching phase and that we should never assume bigger is better in all environments. Additional maternal effects also contributed to the hatching success of offspring in the Pine and Sydenham Rivers, while additive genetic effects were not apparent. Thus far, no in-situ study has been able to partition the variation in hatching success between genetic and maternal sources (Johnson, Roni, & Pess, 2012; Roni et al., 2016). It appears that maternal and environmental effects are the primary determinants of hatching success in the study populations. An important next step is to understand how egg size selection operating at hatching can impact the phenotypic variation available to selection at later life stages.

The effect of egg size on hatching success can have population-level consequences for salmon populations (Chapter 4). More specifically, the match between a population's egg size distribution and the egg size selection gradient can significantly affect the number of live alevins produced by a population. Few studies have assessed how maternal effects may influence population-level processes in fishes (Marteinsdottir & Thorarinsson, 1998; Shaw, Sass, & VanDeHey, 2018; Venturelli, Shuter, & Murphy, 2009; Venturelli et al., 2010). Venturelli et al. (2010) used simulations to show that the selective harvest of older walleye from a population could decrease recruitment because of the positive relationship between juvenile survival, egg size, and maternal size/age. This prediction was supported by Lake Erie walleye, where recruitment was highest when the female age composition was older. In the case of salmon, early life history survival has been incorporated in population matrix models (e.g., Leslie matrix model) and shown to be an important factor influencing population growth rates (Eldridge, Hard, & Naish, 2010; Kareiva, Marvier, & McClure, 2000); however, specific processes affecting early life survival have generally not been considered (but see Greene &

Beechie, 2004). My work has shown that the egg size-survival relationship can greatly influence the number of hatched alevins in a salmon population and, by extension, the number of potential recruits to the spawning stock biomass. My research builds on previous simulations by incorporating both linear and non-linear egg size – survival relationships, which can affect a population in different ways depending on the population egg size distribution. Overall, maternal effects could have a significant effect on the stock – recruitment relationship, and maternal effects should be considered when developing such models for research or management.

## 5.3 Management Implications

The connection between egg mass and population production has implications for salmon management and restoration programs throughout their native and introduced ranges. Any type of selective fishing practice, whether through gear choice or management action, can alter adult phenotypic frequencies in a population by harvesting a specific subset of the population (Kuparinen & Merilä, 2007; Olsen et al., 2004; Olsen et al., 2005; Ricker, 1981). The alteration of adult phenotypic frequencies, such as female length, could have a negative impact on population production by shifting the egg mass distribution of the population away from the phenotypic optimum and reduce early life survival (i.e., indirectly through female size). For example, a management agency may place a minimum size limit on a heavily harvested population of salmon, which could shift the population length distribution towards smaller individuals and, if the egg mass selection gradient is positive and linear, lead to reduced population productivity through poor hatching success. Therefore, management agencies should carefully consider the possible consequences of any management action that alters maternal phenotypes linked to reproduction and/or offspring fitness.

Restoration programs often rely on hatchery operations to supplement small extant populations or to re-establish extinct populations by introducing individuals from another source. Hatchery supplementation operations can be selective when collecting brood stock depending on when collections begin (e.g., phenology) and how individuals are chosen (e.g., morphology; McLean, Bentzen, & Quinn, 2005). The potential genetic effects of selective collections have been well documented (Araki & Schmid, 2010;

Reisenbichler & Rubin, 1999; Utter, 1998). However, the selective collection of individuals can also alter egg mass distributions and, as a result, the reproductive potential of the stocked individuals. When re-establishing a population, reintroduction programs often consider whether a source population is an environmental or genetic match to the restoration habitat (Houde, Garner, & Neff, 2015; Krueger, Gharrett, Dehring, & Allendorf, 1981). A further consideration should be whether the egg size of a source population is matched to the incubation environment of the restoration habitat (i.e., egg size that maximizes survival). Given the link between early life survival and population production, the success of a restoration program could be impeded if maternal effects are not considered when implementing a restoration strategy.

## 5.4 Conclusion

My dissertation has shown that egg size explains the majority of the within and among population variation in offspring phenotypes; determined that egg fatty acid and proximate composition can exert temperature dependent transgenerational effects on offspring phenotypes; and demonstrated the significant affect egg size can have on the hatching success of salmonids in the wild. Importantly, I quantified the contribution of specific maternal effect traits to offspring phenotypes and, as a result, revealed that maternal effects are an important potential pathway through which offspring phenotypes may respond to selection. Furthermore, my work also established that selection acting on egg size during early life can have population-level consequences by altering the production of hatched alevins. Taken together, my dissertation has advanced our understanding of maternal effects and the evolution of salmon, while also providing future avenues of research.

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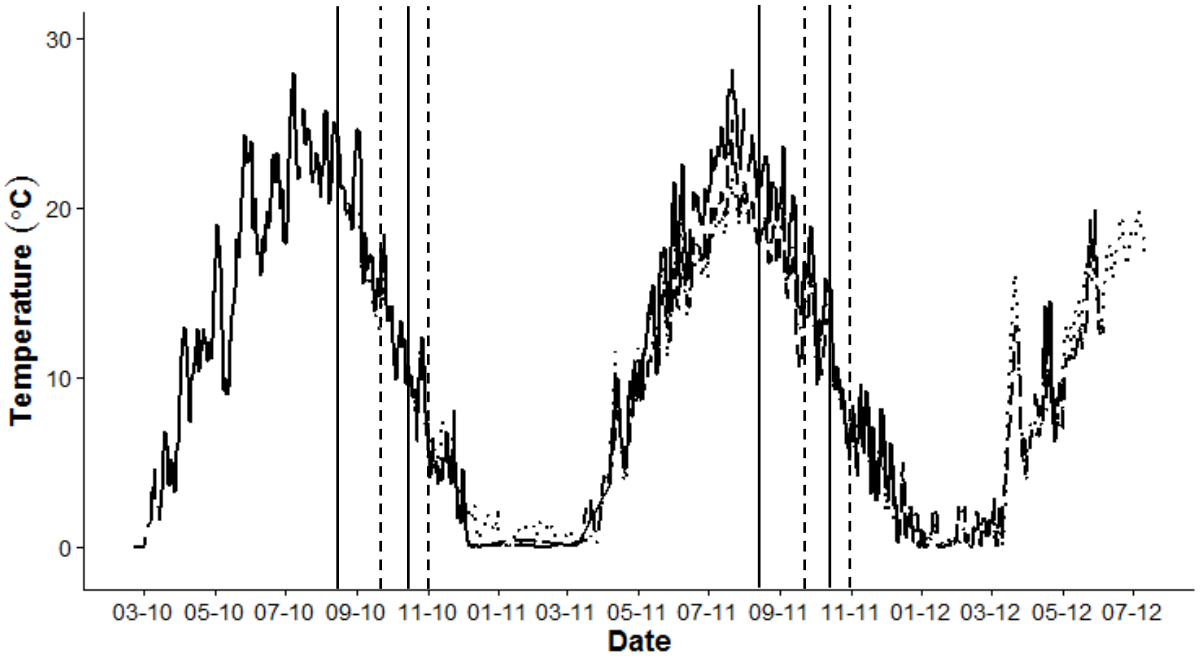
# Appendices

## Appendix A




**Appendix A.1:** The temperature profiles from the Credit (solid), Pine (dash), and Sydenham (dotted) Rivers between 20 February 2010 and 11 July 2012. The dates are presented as month-year. Not all river systems have data for the entire duration of the graphed time period. The approximate spawning times for the three populations are indicated with vertical lines (solid = Pine River; dashed = Credit and Sydenham Rivers). The leftmost vertical lines represent the beginning of the spawning event for a given population and the rightmost represent the end of the spawning event. The Pine River and Sydenham River temperature data was collected using HOBO temperature loggers by M. Thorn and the Credit River temperature data was provided by the Credit Valley Conservation Authority.

**Appendix A.2:** The number of families (# Fam.) and offspring (# Off.) used in the analysis yolk sac volume (YSV), hatch length (HL), swim-up length (SL), juvenile length (JL), yolk sac conversion efficiency (YSCE), hatch to swim-up growth (HSGR), and swim-up to juvenile growth (SJGR). The sample sizes are provided for each population and temperature treatment.

| | | **Credit River** | | **Pine River** | | **Sydenham River** | | **Total** | |
|---|---|---|---|---|---|---|---|---|---|
| **Temp.** | **Trait** | **# Fam.** | **# Off.** | **# Fam.** | **# Off.** | **# Fam.** | **# Off.** | **# Fam.** | **# Off.** |
| 6.5 °C | YSV | 20 | 898 | 25 | 1061 | 22 | 1151 | 67 | 3110 |
| | HL | 20 | 917 | 25 | 1124 | 22 | 1187 | 67 | 3228 |
| | SL | 20 | 644 | 25 | 839 | 22 | 779 | 67 | 2262 |
| | JL | 20 | 628 | 26 | 843 | 22 | 792 | 68 | 2263 |
| | YSCE* | 20 | 20 | 24 | 24 | 22 | 22 | 66 | 66 |
| | HSGR* | 20 | 20 | 24 | 24 | 22 | 22 | 66 | 66 |
| | SJGR* | 20 | 20 | 25 | 25 | 22 | 22 | 67 | 67 |
| 9.4 °C | YSV | 20 | 1119 | 23 | 1106 | 20 | 1147 | 63 | 3372 |
| | HL | 20 | 1136 | 23 | 1168 | 20 | 1194 | 63 | 3498 |
| | SL | 20 | 686 | 26 | 779 | 21 | 717 | 67 | 2182 |
| | JL | 20 | 641 | 26 | 834 | 22 | 799 | 68 | 2274 |
| | YSCE* | 20 | 20 | 23 | 23 | 19 | 19 | 62 | 62 |
| | HSGR* | 20 | 20 | 23 | 23 | 19 | 19 | 62 | 62 |
| | SJGR* | 20 | 20 | 26 | 26 | 21 | 21 | 67 | 67 |
| 15.2 °C | YSV | 14 | 500 | 24 | 418 | 22 | 810 | 60 | 1728 |
| | HL | 14 | 627 | 24 | 808 | 22 | 984 | 60 | 2419 |
| | SL | 20 | 640 | 26 | 800 | 22 | 733 | 68 | 2173 |
| | YSCE* | 14 | 14 | 24 | 24 | 22 | 22 | 60 | 60 |
| | HSGR* | 14 | 14 | 24 | 24 | 22 | 22 | 60 | 60 |

*Measurements of the growth traits were derived from family means. Therefore, the number of families used is equal to the number of offspring.

**Appendix A.3:** Yolk sac volume ($mm^3$; YSV), hatch length (mm; HL), swim-up length (mm; SL), juvenile length (mm; JL), yolk sac conversion efficiency ($mm/mm^3$; YSCE), hatch to swim-up growth (mm/ΔD; HSGR), and swim-up to juvenile growth (mm/ΔD; SJGR) of progeny from the Credit River, Pine River, and Sydenham River when reared under three different thermal regimes. Data are presented as mean ± standard error. YSCE, HSGR, and SJGR were multiplied by 100 for presentation purposes.

| Temp. | Trait | Credit | Pine | Sydenham |
|---|---|---|---|---|
| 6.5 °C | YSV | 223.7 (10.1) | 115.4 (5.7) | 146.7 (7.0) |
| | HL | 22.8 (0.2) | 21.2 (0.2) | 21.7 (0.1) |
| | SL | 32.5 (0.3) | 30.0 (0.2) | 30.8 (0.2) |
| | JL | 38.1 (0.3) | 34.3 (0.4) | 36.0 (0.3) |
| | YSCE | 4.5 (0.2) | 8.1 (0. 5) | 6.5 (0. 3) |
| | HSGR | 3.4 (0.05) | 3.1 (0.04) | 3.3 (0.04) |
| | SJGR | 2.1 (0.08) | 1.7 (0.07) | 1.9 (0.08) |
| 9.4 °C | YSV | 227.6 (9.5) | 114.5 (6.7) | 129.8 (7.1) |
| | HL | 22.2 (0.1) | 21.1 (0.2) | 21.3 (0.2) |
| | SL | 32.8 (0.2) | 30.7 (0.2) | 31.0 (0.2) |
| | JL | 37.6 (0.3) | 34.2 (0.4) | 35.7 (0.3) |
| | YSCE | 4.8 (0. 2) | 9.3 (0. 6) | 7.8 (0. 5) |
| | HSGR | 3.4 (0.05) | 3.3 (0.03) | 3.2 (0.03) |
| | SJGR | 1.7 (0.08) | 1.2 (0. 1) | 1.6 (0.08) |
| 15.2 °C | YSV | 129.7 (6.6) | 82.9 (4.0) | 106.7 (6.0) |
| | HL | 20.4 (0.2) | 18.8 (0.2) | 19.3 (0.1) |
| | SL | 29.5 (0.2) | 28.2 (0.2) | 27.4 (0.2) |
| | YSCE | 7.4 (0. 4) | 11.7 (0. 5) | 8.1 (0. 5) |
| | HSGR | 3.6 (0.07) | 3.6 (0.07) | 3.1 (0.04) |

**Appendix A.4:** The sire variance (Vs), dam variance (Vd), cup variance (Vc), environmental variance (Ve), heritability ($h^2$), and maternal effects (m) for hatch length (HL), yolk sac volume (YSV), swim-up length (SL), and juvenile length (JL) at each temperature treatment. The cup variance is present only for the hatching traits because family pairs were split at the swim-up stage for sampling/further rearing. The heritability was calculated as the proportion of phenotypic variance explained by additive genetic effects (4*(Vs/Vs+Vd+Vc+Ve)). The maternal effects were calculated as the proportion of phenotypic variance explained by dam identity minus the variance explained by sire identity ((Vd-Vs)/Vs+Vd+Vc+Ve). The quantitative genetic components were calculated using a model without egg size as a covariate (Base) and with egg size included as a covariate (Egg). Values in the brackets are the bias corrected and accelerated bootstrap 95% confidence intervals. The significance of the sire and dam random effects in the models were tested using a simulation-based restricted likelihood ratio test ($P < 0.05 = *$; $P \geq 0.05 = ^{ns}$).

| Trait | Model | Temp. | Vs | Vd | Vc | Ve | $h^2$ | m |
|---|---|---|---|---|---|---|---|---|
| HL | Base | 6.5 °C | 0.02 (0 - 0.05) | **0.46 (0.42 - 0.51)** | 0.10 (0.08 - 0.11) | 0.32 (0.31 - 0.36) | 0.08 (0 - 0.21) | 0.49 (0.42 - 0.55) |
| | | 9.4 °C | **0.13 (0.10 - 0.16)** | **0.28 (0.24 - 0.33)** | 0.07 (0.06 - 0.08) | 0.27 (0.26 - 0.29) | 0.69 (0.54 - 0.84) | 0.20 (0.12 - 0.28) |
| | | 15.2 °C | 0.02 (0 - 0.07) | **0.40 (0.33 - 0.47)** | 0.13 (0.11 - 0.15) | 0.48 (0.47 - 0.51) | 0.07 (0 - 0.28) | 0.37 (0.26 - 0.44) |
| YSV | | 6.5 °C | 66.6 (0 - 167.4) | **994.0 (873.0 - 1124.1)** | 314.8 (211.9 - 344.3) | 1318.1 (1303 - 1415) | 0.10 (0 - 0.25) | 0.34 (0.28 - 0.40) |
| | | 9.4 °C | **562.8 (485.3 – 644.5)** | **542.9 (462.6 - 626.7)** | 319.0 (252.7 - 342.8) | 911.2 (897.2 - 970.3) | 0.96 (0.84 - 1.1) | 0.0 (0.0 - 0.05) |
| | | 15.2 °C | 0.0003 (0.0 – 0.92) | **446.2 (390.8 - 503.7)** | 161.8 (107.3 - 181.1) | 546.1 (534.7 - 597.6) | 0.000001 (0 - 0.004) | 0.39 (0.34 - 0.43) |
| SL | | 6.5 °C | 0.08 (0.02 - 0.13) | **1.08 (0.98 - 1.17)** | - | 0.43 (0.36 - 0.59) | 0.19 (0.04 - 0.33) | 0.64 (0.56 - 0.70) |
| | | 9.4 °C | 0.11 (0.07 - 0.15) | **0.98 (0.89 - 1.07)** | - | 0.27 (0.26 - 0.30) | 0.31 (0.19 - 0.44) | 0.65 (0.57 - 0.71) |
| | | 15.2 °C | 0.19 (0.14 - 0.24) | **0.71 (0.62 - 0.79)** | - | 0.39 (0.37 - 0.46) | 0.59 (0.45 - 0.74) | 0.40 (0.32 - 0.47) |
| JL | | 6.5 °C | 0.20 (0.03 - 0.36) | **2.33 (2.01 - 2.52)** | - | 2.25 (2.12 - 2.63) | 0.17 (0.03 - 0.31) | 0.45 (0.37 - 0.50) |
| | | 9.4 °C | **0.70 (0.52 - 0.88)** | **2.01 (1.65 - 2.26)** | - | 2.69 (2.56 - 2.99) | 0.52 (0.40 - 0.64) | 0.24 (0.16 - 0.29) |
| HL | Egg | 6.5 °C | 0.01 (0.0 – 0.03) | **0.11 (0.08 – 0.14)** | 0.10 (0.08 – 0.11) | 0.32 (0.31 – 0.36) | 0.10 (0.0 – 0.25) | 0.18 (0.10 – 0.25) |
| | | 9.4 °C | **0.04 (0.03 – 0.06)** | **0.05 (0.03 – 0.07)** | 0.07 (0.06 – 0.08) | 0.27 (0.26 – 0.29) | 0.39 (0.24 – 0.53) | 0.01 (-0.06 – 0.09) |
| | | 15.2 °C | 0.004 (0.0 – 0.05) | **0.21 (0.15 – 0.27)** | 0.14 (0.10 – 0.15) | 0.48 (0.47 – 0.51) | 0.02 (0.0 – 0.23) | 0.25 (0.16 – 0.32) |
| YSV | | 6.5 °C | 0.0004 (0.0004 – 28.1) | **171.3 (99.8 – 243.6)** | 313.0 (219.7 – 340.7) | 1319.8 (1303 – 1406) | 0.0000009 (0.0 – 0.07) | 0.10 (0.06 – 0.14) |
| | | 9.4 °C | 142.9 (93.8 – 196.9) | **132.3 (68.9 – 196.1)** | 313.6 (251.5 – 336.0) | 911.4 (898.0 – 964.5) | 0.38 (0.25 – 0.52) | -0.007 (-0.08 – 0.06) |
| | | 15.2 °C | 23.5 (0.0 – 62.8) | 80.5 (33.7 – 129.5) | 162.2 (110.4 – 180.2) | 545.5 (532.3 – 601.2) | 0.12 (0.0 – 0.31) | 0.07 (-0.02 – 0.15) |
| SL | | 6.5 °C | 0.05 (0.02 – 0.09) | **0.21 (0.17 – 0.24)** | - | 0.43 (0.36 – 0.59) | 0.30 (0.12 – 0.49) | 0.23 (0.13 – 0.30) |
| | | 9.4 °C | 0.05 (0.03 – 0.08) | **0.22 (0.17 – 0.24)** | - | 0.27 (0.26 – 0.30) | 0.38 (0.20 – 0.57) | 0.31 (0.20 – 0.38) |
| | | 15.2 °C | **0.21 (0.16 – 0.26)** | **0.22 (0.16 – 0.25)** | - | 0.39 (0.37 – 0.45) | 1.02 (0.81 – 1.23) | 0.01 (-0.09 – 0.09) |
| JL | | 6.5 °C | **0.36 (0.22 – 0.50)** | **0.82 (0.60 – 0.91)** | - | 2.24 (2.12 – 2.63) | 0.42 (0.25 – 0.58) | 0.14 (0.04 – 0.19) |
| | | 9.4 °C | **0.67 (0.53 – 0.81)** | **0.96 (0.63 – 1.23)** | - | 2.69 (2.57 – 2.96) | 0.62 (0.49 – 0.75) | 0.07 (-0.02 – 0.13) |

# Appendix B

**Appendix B.1:** Number of families used for the analysis of hatch length, swim-up length, and growth by population and temperature.

| Temp | Trait | Credit | Pine | Sydenham |
|---|---|---|---|---|
| 6.5 | Hatch length | 18 | 25 | 21 |
| | Swim-up | 18 | 25 | 21 |
| | growth | 18 | 24 | 21 |
| 9.4 | Hatch length | 18 | 23 | 19 |
| | Swim-up | 18 | 26 | 20 |
| | growth | 18 | 23 | 18 |
| 15.2 | Hatch length | 13 | 24 | 21 |
| | Swim-up | 18 | 26 | 21 |
| | growth | 13 | 24 | 21 |

**Appendix B.2:** The mean (± SE) hatch length (HL), swim-up length (SWL), and hatch to swim-up growth rate (HSG) of Chinook salmon (*Oncorhynchus tshawytscha*) progeny from the Credit (CR), Pine (PR), and Sydenham Rivers (SR) at each temperature. Hatch success (HS) and hatch to swim-up survival (HSS) are presented as the median (minimum-maximum).

| Temperature | Trait | CR | PR | SR |
|---|---|---|---|---|
| 6.5 °C | HL (mm) | 22.82 ± 0.16 | 21.17 ± 0.18 | 21.68 ± 0.14 |
| | SWL (mm) | 32.55 ± 0.28 | 29.95 ± 0.23 | 30.80 ± 0.20 |
| | HSG ($mm \cdot \Delta D^{-1}$) | 0.034 ± 0.001 | 0.031 ± 0.001 | 0.032 ± 0.001 |
| | HS (%) | 93.4 (65.9-100) | 97.5 (66.6-100) | 98.8 (81.9-100) |
| | HSS (%) | 100 (90.0-100) | 100 (87.3-100) | 100 (95.1-100) |
| 9.4 °C | HL (mm) | 22.28 ± 0.12 | 21.06 ± 0.17 | 21.30 ± 0.16 |
| | SWL (mm) | 32.84 ± 0.24 | 30.67 ± 0.24 | 30.99 ± 0.20 |
| | HSG ($mm \cdot \Delta D^{-1}$) | 0.034 ± 0.001 | 0.033 ± 0.001 | 0.031 ± 0.001 |
| | HS (%) | 97.3 (89.1-100) | 97.5 (42.5-100) | 97.2 (81.0-100) |
| | HSS (%) | 98.7 (76.3-100) | 99.4 (56.4-100) | 100 (50.0-100) |
| 15.2 °C | HL (mm) | 20.32 ± 0.20 | 18.83 ± 0.16 | 19.28 ± 0.15 |
| | SWL (mm) | 29.48 ± 0.23 | 28.16 ± 0.21 | 27.39 ± 0.19 |
| | HSG ($mm \cdot \Delta D^{-1}$) | 0.036 ± 0.001 | 0.036 ± 0.001 | 0.031 ± 0.001 |
| | HS (%) | 95.0 (59.2-100) | 92.5 (69.1-100) | 95.0 (72.7-100) |
| | HSS (%) | 98.8 (78.6-100) | 96.0 (45.2-100) | 97.3 (45.2-100) |

**Appendix B.3:** Parameters, loglikelihood values, and p-values of models tested during the model selection procedure for hatch length, swim-up length, and growth rate. A backwards model selection procedure was used, whereby the weakest interaction was iteratively removed until the loglikelihood of the nested model was significantly reduced relative to the model before. Bolded models indicate the final selected model.

| Trait | Model | Loglikelihood | p-value |
|---|---|---|---|
| Hatch Length | Pop + Temp + Egg + PC1 + Lipid + Pop x Temp + Pop x Egg + Temp x Egg + Pop x PC1 + Temp x PC1 + Pop x Lipid + Temp x Lipid | -94.08 | - |
| | Pop + Temp + Egg + PC1 + Lipid + Pop x Temp + Pop x Egg + Pop x PC1 + Temp x PC1 + Pop x Lipid + Temp x Lipid | -94.71 | 0.53 |
| | Pop + Temp + Egg + PC1 + Lipid + Pop x Egg + Pop x PC1 + Temp x PC1 + Pop x Lipid + Temp x Lipid | -95.99 | 0.62 |
| | **Pop + Temp + Egg + PC1 + Lipid + Pop x Egg + Pop x PC1 + Temp x PC1 + Pop x Lipid** | **-96.69** | **0.49** |
| | Pop + Temp + Egg + PC1 + Lipid + Pop x Egg + Pop x PC1 + Pop x Lipid | -100.36 | 0.025 |
| Swim-Up Length | Pop + Temp + Egg + PC1 + Lipid + Pop x Temp + Pop x Egg + Temp x Egg + Pop x PC1 + Temp x PC1 + Pop x Lipid + Temp x Lipid | -119.16 | - |
| | Pop + Temp + Egg + PC1 + Lipid + Pop x Temp + Pop x Egg + Temp x Egg + Pop x PC1 + Pop x Lipid + Temp x Lipid | -119.31 | 0.86 |
| | Pop + Temp + Egg + PC1 + Lipid + Pop x Temp + Pop x Egg + Temp x Egg + Pop x PC1 + Temp x Lipid | -120.70 | 0.25 |
| | Pop + Temp + Egg + PC1 + Lipid + Pop x Temp + Pop x Egg + Temp x Egg + Pop x PC1 | -121.62 | 0.40 |
| | **Pop + Temp + Egg + PC1 + Pop x Temp + Pop x Egg + Temp x Egg + Pop x PC1** | **-121.69** | **0.72** |
| | Pop + Temp + Egg + PC1 + Pop x Temp + Pop x Egg + Pop x PC1 | -131.79 | < 0.0001 |
| Growth Rate | Pop + Temp + Egg + PC1 + Lipid + Pop x Temp + Pop x Egg + Temp x Egg + Pop x PC1 + Temp x PC1 + Pop x Lipid + Temp x Lipid | 902.58 | - |
| | Pop + Temp + Egg + PC1 + Lipid + Pop x Temp + Pop x Egg + Temp x Egg + Pop x PC1 + Pop x Lipid + Temp x Lipid | 902.33 | 0.78 |
| | Pop + Temp + Egg + PC1 + Lipid + Pop x Temp + Pop x Egg + Temp x Egg + Pop x Lipid + Temp x Lipid | 902.09 | 0.78 |
| | Pop + Temp + Egg + Lipid + Pop x Temp + Pop x Egg + Temp x Egg + Pop x Lipid + Temp x Lipid | 901.27 | 0.20 |
| | **Pop + Temp + Egg + Lipid + Pop x Temp + Pop x Egg + Pop x Lipid + Temp x Lipid** | **899.13** | **0.12** |
| | Pop + Temp + Egg + Lipid + Pop x Temp + Pop x Lipid + Temp x Lipid | 895.82 | 0.036 |

**Appendix B.4:** Parameter estimates, standard error (SE), and t-statistic for the hatch length linear mixed model. Interactions between variables are indicated with a ":" between parameters. The Credit River population and the 6.5°C treatment served as the contrasts for the model.

| Parameter | Estimate | SE | t-value |
|---|---|---|---|
| Intercept | 20.16 | 0.90 | 22.45 |
| Temp. – 9.4°C | -0.35 | 0.07 | -4.82 |
| Temp. – 15.2°C | -2.38 | 0.07 | -32.65 |
| Pop. – Pine | -3.42 | 1.04 | -3.29 |
| Pop. – Sydenham | 0.40 | 1.10 | 0.36 |
| Egg Mass | 10.27 | 1.74 | 5.91 |
| PC1 | 0.09 | 0.05 | 1.79 |
| Lipid | -3.65 | 4.23 | -0.86 |
| Pop. – Pine : Egg Mass | 10.20 | 2.69 | 3.79 |
| Pop. – Sydenham : Egg mass | 3.46 | 2.63 | 1.31 |
| Temp. – 9.4°C : PC1 | -0.06 | 0.03 | -2.23 |
| Temp. – 15.2°C : PC1 | -0.06 | 0.03 | -2.28 |
| Pop. – Pine : PC1 | -0.11 | 0.06 | -1.92 |
| Pop. – Sydenham : PC1 | -0.18 | 0.06 | -2.87 |
| Pop. – Pine : Lipid | 9.26 | 5.58 | 1.66 |
| Pop. – Sydenham : Lipid | -10.40 | 5.93 | -1.75 |

**Appendix B.5:** Parameter estimates, standard error (SE), and t-statistic for the swim-up length linear mixed model. Interactions between variables are indicated with a ":" between parameters. The Credit River population and the 6.5°C treatment served as the contrasts for the model.

| Parameter | Estimate | SE | t-value |
|---|---|---|---|
| Intercept | 24.80 | 0.63 | 39.33 |
| Temp. – 9.4°C | 1.16 | 0.53 | 2.19 |
| Temp. – 15.2°C | -0.81 | 0.53 | -1.53 |
| Pop. – Pine | -2.45 | 0.75 | -3.28 |
| Pop. – Sydenham | 1.05 | 0.80 | 1.31 |
| Egg Mass | 24.37 | 2.02 | 12.05 |
| PC1 | 0.26 | 0.05 | 5.08 |
| Pop. – Pine : Egg Mass | 16.96 | 2.91 | 5.83 |
| Pop. – Sydenham : Egg mass | -0.74 | 3.12 | -0.24 |
| Temp. – 9.4°C : Egg Mass | -3.09 | 1.81 | -1.71 |
| Temp. – 15.2°C : Egg Mass | -7.97 | 1.81 | -4.41 |
| Temp. – 9.4°C : Pop. – Pine | 0.21 | 0.26 | 0.83 |
| Temp. – 9.4°C : Pop. – Sydenham | 0.53 | 0.26 | 2.09 |
| Temp. – 15.2°C : Pop. – Pine | -0.31 | 0.23 | -1.39 |
| Temp. – 15.2°C : Pop. – Sydenham | -0.95 | 0.22 | -4.25 |
| Pop. – Pine : PC1 | -0.36 | 0.07 | -5.52 |
| Pop. – Sydenham : PC1 | -0.35 | 0.07 | -4.85 |

**Appendix B.6:** Parameter estimates, standard error (SE), and t-statistic for the growth rate linear mixed model. Interactions between variables are indicated with a ":" between parameters. The Credit River population and the 6.5°C treatment served as the contrasts for the model.

| Parameter | Estimate | SE | t-value |
|---|---|---|---|
| Intercept | 0.022 | 0.004 | 5.73 |
| Temp. – 9.4°C | -0.005 | 0.003 | -1.92 |
| Temp. – 15.2°C | -0.008 | 0.003 | -3.11 |
| Pop. – Pine | 0.006 | 0.004 | 1.44 |
| Pop. – Sydenham | 0.008 | 0.004 | 1.90 |
| Egg Mass | 0.033 | 0.007 | 4.85 |
| Lipid | 0.021 | 0.019 | 1.10 |
| Pop. – Pine : Egg Mass | 0.012 | 0.010 | 1.19 |
| Pop. – Sydenham : Egg mass | -0.014 | 0.010 | -1.40 |
| Temp. – 9.4°C : Pop. – Pine | 0.002 | 0.0007 | 3.21 |
| Temp. – 9.4°C : Pop. – Sydenham | 0.004 | 0.0008 | 5.15 |
| Temp. – 15.2°C : Pop. – Pine | 0.0004 | 0.0008 | 0.50 |
| Temp. – 15.2°C : Pop. – Sydenham | -0.002 | 0.0008 | -1.90 |
| Temp. – 9.4°C : Lipid | 0.030 | 0.019 | 1.60 |
| Temp. – 15.2°C : Lipid | 0.067 | 0.018 | 3.66 |
| Pop. – Pine : Lipid | -0.060 | 0.022 | -2.78 |
| Pop. – Sydenham : Lipid | -0.038 | 0.023 | -1.70 |

# Appendix C

**Appendix C.1:** Loadings, eigenvalues, and the proportion of variation explained for the first three axes from a principal component analysis (PCA) of the incubator gravel composition in the Credit River. The gravel composition is equal to the proportion of sediment by weight from each substrate class (particle diameter).

| **Substrate Class** | **PC1** | **PC2** | **PC3** |
|---|---|---|---|
| Coarse Gravel (≥ 31.5 mm) | 0.29 | 0.39 | 0.48 |
| Medium Gravel (16 mm) | 0.34 | -0.13 | -0.65 |
| Fine Gravel (8 mm) | -0.18 | -0.54 | -0.13 |
| Very Fine Gravel (4 mm) | -0.42 | -0.28 | 0.24 |
| Very Coarse Sand (2 mm) | -0.32 | -0.27 | -0.02 |
| Coarse Sand (1 mm) | -0.37 | 0.23 | -0.09 |
| Medium Sand (0.5 mm) | -0.44 | 0.19 | 0.09 |
| Fine Sand (0.125 mm) | -0.35 | 0.31 | -0.23 |
| Very Fine Sand (< 0.125 mm) | -0.18 | 0.46 | -0.45 |
| Eigenvalue | 3.83 | 2.67 | 1.15 |
| Proportion of Variation | 0.43 | 0.30 | 0.13 |

**Appendix C.2:** Loadings, eigenvalues, and the proportion of variation explained for the first three axes from a principal component analysis (PCA) of the incubator gravel composition in the Pine River. The gravel composition is equal to the proportion of sediment by weight from each substrate class (particle diameter).

| **Substrate Class** | **PC1** | **PC2** | **PC3** |
|---|---|---|---|
| Coarse Gravel (≥ 31.5 mm) | 0.30 | -0.23 | 0.51 |
| Medium Gravel (16 mm) | 0.20 | -0.02 | -0.75 |
| Fine Gravel (8 mm) | -0.43 | -0.11 | 0.26 |
| Very Fine Gravel (4 mm) | -0.46 | 0.09 | 0.04 |
| Very Coarse Sand (2 mm) | -0.34 | 0.34 | -0.22 |
| Coarse Sand (1 mm) | -0.04 | 0.62 | 0.09 |
| Medium Sand (0.5 mm) | 0.18 | 0.55 | 0.19 |
| Fine Sand (0.125 mm) | 0.39 | 0.34 | 0.12 |
| Very Fine Sand (< 0.125 mm) | 0.39 | -0.05 | -0.06 |
| Eigenvalue | 4.16 | 1.82 | 1.45 |
| Proportion of Variation | 0.46 | 0.20 | 0.16 |

**Appendix C.3:** Loadings, eigenvalues, and the proportion of variation explained for the first three axes from a principal component analysis (PCA) of the incubator gravel composition in the Sydenham River. The gravel composition is equal to the proportion of sediment by weight from each substrate class (particle diameter).

| **Substrate Class** | **PC1** | **PC2** | **PC3** |
|---|---|---|---|
| Coarse Gravel (≥ 31.5 mm) | -0.18 | 0.27 | -0.75 |
| Medium Gravel (16 mm) | 0.37 | 0.10 | 0.45 |
| Fine Gravel (8 mm) | -0.31 | -0.47 | -0.06 |
| Very Fine Gravel (4 mm) | -0.35 | -0.39 | 0.13 |
| Very Coarse Sand (2 mm) | -0.39 | -0.21 | 0.27 |
| Coarse Sand (1 mm) | -0.39 | 0.11 | 0.18 |
| Medium Sand (0.5 mm) | -0.41 | 0.20 | -0.01 |
| Fine Sand (0.125 mm) | -0.34 | 0.41 | 0.14 |
| Very Fine Sand (< 0.125 mm) | -0.18 | 0.53 | 0.31 |
| Eigenvalue | 5.10 | 1.52 | 1.27 |
| Proportion of Variation | 0.57 | 0.17 | 0.14 |

**Appendix C.4:** Loadings, eigenvalues, and the proportion of variation explained for the first three axes from a principal component analysis (PCA) of the incubator gravel composition across the Credit, Pine, and Sydenham Rivers. The gravel composition is equal to the proportion of sediment by weight from each substrate class (particle diameter).

| **Substrate Class** | **PC1** | **PC2** | **PC3** |
|---|---|---|---|
| Coarse Gravel (≥ 31.5 mm) | 0.01 | 0.43 | 0.66 |
| Medium Gravel (16 mm) | -0.42 | -0.09 | -0.41 |
| Fine Gravel (8 mm) | 0.35 | -0.20 | 0.37 |
| Very Fine Gravel (4 mm) | 0.41 | -0.29 | 0.07 |
| Very Coarse Sand (2 mm) | 0.40 | -0.26 | -0.15 |
| Coarse Sand (1 mm) | 0.39 | -0.06 | -0.22 |
| Medium Sand (0.5 mm) | 0.38 | 0.20 | -0.30 |
| Fine Sand (0.125 mm) | 0.22 | 0.53 | -0.23 |
| Very Fine Sand (< 0.125 mm) | 0.16 | 0.54 | -0.19 |
| Eigenvalue | 4.44 | 2.01 | 1.06 |
| Proportion of Variation | 0.49 | 0.22 | 0.12 |

# Appendix D

The following are approval letters from the Western University Animal Use Subcommittee for Animal Use Protocol # 2007-043-05, which covered all procedures performed on animals during the execution of my research.

Western

2007-043-05::5:

**AUP Number:** 2007-043-05
**AUP Title:** Evolutionary Biology and Ecology of Early Development in Salmon

**Approval Date:** 07/28/2011

The YEARLY RENEWAL to Animal Use Protocol (AUP) 2007-043-05 has been approved.

1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. 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.

Submitted by: Kinchlea, Will D

on behalf of the Animal Use Subcommittee

*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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Western

2007-043-05::6:

**AUP Number:** 2007-043-05
**AUP Title:** Evolutionary Biology and Ecology of Early Development in Salmon

**Yearly Renewal Date:** 08/01/2013

**The YEARLY RENEWAL to Animal Use Protocol (AUP) 2007-043-05 has been approved, and will be approved for one year following the above review date.**

1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. 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.

Submitted by: Kinchlea, Will D
on behalf of the Animal Use Subcommittee

*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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Western

2007-043-05::7:

**AUP Number:** 2007-043-05
**AUP Title:** Evolutionary Biology and Ecology of Early Development in Salmon

**Yearly Renewal Date:** 08/01/2014

**The YEARLY RENEWAL to Animal Use Protocol (AUP) 2007-043-05 has been approved, and will be approved for one year following the above review date.**

1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. 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.

Submitted by: Kinchlea, Will D
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*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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# Curriculum Vitae

**Name:** Michael Thorn

**Post-secondary Education and Degrees:**

Lakehead University
Orillia, Ontario, Canada
2006-2010 H.B.A.Sc.

Lakehead University
Thunder Bay, Ontario, Canada
2010-2011 H.B.Sc.

University of Western Ontario
London, Ontario, Canada
2011-2019 Ph.D. (Environment and Sustainability)

**Honours and Awards:**

Natural Science and Engineering Research Council of Canada (NSERC) Postgraduate Scholarship - PhD
2015 - 2017

Biology Graduate Teaching Award
2016 – 2017

Environment and Sustainability Graduate Student Award
2015

Environment and Sustainability Travel Award
2015

Western University Biology Department Travel Award
2013

Lakehead University Young Alumni Award
2013

NSERC Canada Graduate Scholarship - MSc
2012 – 2013

Lakehead University President's Award
2010

Queen Elizabeth II Aiming for the Top Scholarship
2006 – 2010

**Related Work Experience**

Assessment Biologist
Ontario Ministry of Natural Resources and Forestry
June 2018 – Present

Aquatic Ecosystem Biologist
Ontario Ministry of Natural Resources and Forestry
June 2017 – June 2018

Lake Simcoe Research Biologist
Ontario Ministry of Natural Resources and Forestry
December 2015 – March 2016

Teaching Assistant
The University of Western Ontario
2011 – 2016

Research Assistant
Lakehead University
2009 - 2010

**Publications and Technical Reports:**

**Thorn, M.W.**, Dick, M.F., Oviedo, L., Guglielmo, C.G., & Morbey, Y.E. (2018). Transgenerational effects of egg nutrients on the early development of Chinook salmon (*Oncorhynchus tshawytscha*) across a thermal gradient. *Canadian Journal of Fisheries and Aquatic Sciences* (in press).

**Thorn, M.W.**, & Morbey, Y.E. (2018). Egg size and the adaptive capacity of early life history traits in Chinook salmon (*Oncorhynchus tshawytscha*). *Evolutionary Applications* 11(2): 205-219.

**Thorn, M.W.**, & Morbey, Y.E. (2016). Evidence for the secondary sexual development of the anal fin in female kokanee salmon (*Oncorhynchus nerka*). *Journal of Fish Biology* 88(2): 448-458.

**Thorn, M.W.**, Chu, Cindy, and Jones, N.E. (2016). Influence of environmental variables on the occurrence of brook trout (*Salvelinus fontinalis*) within the Lake Simcoe watershed. Science and Research Technical Report TR-09, Ontario Ministry of Natural Resources and Forestry. 58 pp.

Kanavillil, N., **Thorn, M**., & Kurissery, S. (2012). Characterization of natural biofilms in temperate inland waters. *Journal of Great Lakes Research* 38 (3): 429-438.