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CHANGING ENVIRONMENTAL CONDITIONS AND THE RESPONSE AND  
POTENTIAL ADAPTABILITY OF FRESHWATER WHITEFISHES

A Dissertation Presented

by

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## ABSTRACT

Changes in winter conditions, such as increased temperatures and decreased ice coverage, have been observed worldwide. The responses of many lake fish populations to changing winters are projected to be inadequate to counter the speed and magnitude of climate change. Such environmental changes have been hypothesized to explain the low recruitment observed in freshwater whitefishes (Salmonidae Coregoninae). My research focused on measuring the impact changing winter conditions may have on coregonine reproductive phenology and developmental and morphological traits to better predict changes in coregonine populations as a result of climate change.

I used experimental incubation methods and modeling to explore how climate-induced changes in water temperature and ice coverage may impact coregonine adults during spawning and early-life stages within and among species. First, I experimentally evaluated the response of embryonic development to increasing water temperature for cisco (*Coregonus artedii*) from lakes Superior and Ontario, and vendace (*C. albula*) and European whitefish (*C. lavaretus*) from Lake Southern Konnevesi, Finland. Embryo survival, incubation duration, and length-at-hatch were inversely related to temperature whereas yolk-sac volume increased with temperature within study groups. However, responses varied in magnitude among study groups suggesting differential levels of developmental plasticity. Next, I quantified how cisco embryos from lakes Superior and Ontario responded to simulated changes in incubation light conditions representing 0-10 (high light), 40-60 (medium light), and 90-100% (low light) ice coverage. Embryo survival was highest under medium light, and light intensity had no effect on incubation duration. Increasing light intensity decreased length-at-hatch in Lake Superior but had no effect in Lake Ontario. Yolk-sac volume was positively correlated with increasing light in Lake Superior and negatively correlated in Lake Ontario. Contrasting responses between lakes suggest populations' response to light is flexible. Furthermore, I analyzed different embryo incubation temperatures on post-hatching survival, growth, and critical thermal maximum of larval cisco from lakes Superior and Ontario. Larval survival and critical thermal maximum were negatively related to temperature, and larval growth was positively related to temperature. The magnitude of change was greater in Lake Superior than Lake Ontario for all traits examined, suggesting Lake Superior larvae may possess a more limited ability to acclimate to and cope with environmental change. Lastly, I used simulation modeling to investigate changes in reproductive phenology under climatic-warming scenarios for coregonine populations across the Laurentian Great Lakes and Europe. Models predicted that climate-induced increases in water temperatures may cause delayed spawning, shorter embryo incubation lengths, and earlier larval hatching.

I quantified how climate change could affect coregonine populations, including changes in embryo development traits, reduced physiological condition of larvae, and shifts in reproductive phenology. Climate-induced responses of coregonines to changing environmental conditions are likely to vary within and among species and with the magnitude of climate warming. Management strategies that maximize phenotypic variability could improve the ability of coregonines to cope with environmental change.

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## **CHAPTER 1: COREGONINE HISTORY AND CLIMATE CHANGE IMPACTS**

### **The Coregonine Concern**

Freshwater whitefish, Salmonidae Coregoninae (hereafter coregonines), is a group of 86 cold, stenothermic fish species that occur throughout northern latitudes.

Coregonines hold great cultural importance throughout their range due to the value of both their flesh and roe for human consumption. Historically, coregonines were the most valuable fishery in the waters they inhabited. Sadly, throughout much of their range, a combination of overfishing, invasive species, and habitat changes led to the collapse of many coregonine fisheries in the 20th century (Bogue 2001; Nyberg et al. 2001; Karjalainen et al. 2015). Restoration of these fisheries has been actively occurring worldwide for several decades.

Unfortunately, failing coregonine populations are not restricted to the past. In contemporary times, coregonine fisheries worldwide have experienced population declines due to highly variable and weak year-class strengths (Nyberg et al. 2001; Vonlanthen et al. 2009; Vonlanthen et al. 2012; Anneville et al. 2015). The underlying factors implicit in these weak year-classes are unknown, but winter conditions during embryo incubations and larval hatching are hypothesized to play a role in recruitment success (Nyberg et al. 2001; Marjomäki et al. 2004; Karjalainen et al. 2015; Lynch et al. 2015; Karjalainen, Jokinen, et al. 2016).

Recent coregonine rehabilitation initiatives have placed an emphasis on assessing current knowledge of life history and ongoing impediments to population growth (Bronte

et al. 2017). Our limited understanding of the ecology and life history of coregonines restricts the ability of managers to predict the long-term impact environmental factors may have on coregonine recruitment, growth, and survival. Identifying relationships between climate-controlled variables such as ice formation and water temperatures and coregonine early life-history would be an important step toward improving these restoration efforts worldwide.

### **A Changing World**

Natural systems have been profoundly transformed by human activity since the 1800s (Vitousek 1994), but over the last three decades these changes have accelerated at unprecedented rates (Walther et al. 2002; Struve 2007; Jane et al. 2020; Woolway et al. 2020). Biodiversity is declining more acutely in freshwater systems than in other ecosystems (Sala et al. 2000; Strayer & Dudgeon 2010; Tickner et al. 2020). One of the greatest threats to freshwater systems and biodiversity is climate change and the unprecedented rise of water temperatures on a global scale (Austin & Colman 2008; O'Reilly et al. 2015; Maberly et al. 2020; Woolway et al. 2020).

Ectotherms, such as fish, have specific thermal limits and tolerance ranges (Comte & Olden 2017; Dahlke et al. 2020; Little et al. 2020). Fish that are restricted to lake systems are particularly vulnerable as they have few, if any, opportunities to migrate and evade environmental change due to the isolated nature of lakes. The effects of climate warming on inland fishes are predicted to be highest for spawners, embryos, and larval fish (Dahlke et al. 2020; Sunday 2020).

Understanding fish recruitment variability is a major challenge in fisheries science (Hjort 1914; Miller et al. 1988; Cushing 1990). Despite nearly a century of research on coregonines, our understanding of recruitment dynamics is still limited (Marjomäki et al. 2004; Karjalainen et al. 2015; Myers et al. 2015). Stock-recruitment relationships can be derived from long-term data for many fish species, but how environmental variability can modify stock-recruitment relationships has been difficult to decipher (Eckmann et al. 1988; Marjomäki 2004; Anneville et al. 2009; Bunnell et al. 2010; Lynch et al. 2015). Adding a warming climate to this problem makes it even more difficult to solve.

### **Need to Understand Coregonine Life History**

Coregonines are ecologically and morphologically diverse both within species and among species with similar and contrasting life-history traits (Table 1.1). For example, *Coregonus kiyi* occur only in the deepest of the Laurentian Great Lakes, whereas *C. artedi* and *C. abula*, occur throughout North America and Europe, respectively in a variety of lake types (Eshenroder et al. 2016). This high genetic diversity is reflected in their morphology and in broad ecological differences among species (Table 1.1).

Current and past management goals have included fish community restoration, particularly in the Great Lakes, but management agencies have historically focused rehabilitation efforts on native piscivore species (Hansen et al. 1995; Selgeby et al. 1995; Krueger & Ebener 2004) - little emphasis has been placed on the prey fishes (e.g., cisco) that support most predator populations (e.g., lake trout *Salvelinus namaycush*; Dryer &

Beil, 1964; Stockwell et al., 2009; Zimmerman & Krueger, 2009). However, fishery managers have recently expressed interest in reestablishing a native forage base in the Great Lakes to support the critical role native prey fish play in Great Lakes food webs and energy transfer within the benthic and pelagic communities, with coregonines broadly serving as the priority group of species (Zimmerman & Krueger 2009; Bronte et al. 2017).

Recent coregonine rehabilitation initiatives have placed an emphasis on assessing current knowledge of life history and ongoing impediments to population growth, prior to implementing restoration plans (Bronte et al. 2017). Our limited understanding of the ecology and life history of coregonines restricts the ability of managers to predict the long-term impact environmental factors may have on coregonine recruitment, growth, and survival. Thus, adaptive management plans are guiding systematic research to better understand the genetic and ecological basis of coregonines around the globe.

### **A Better Understanding**

For my dissertation, I led a team of collaborators to explore how climate-induced changes in water temperature and ice coverage may impact coregonine early-life stages and reproductive phenology. In Chapter 2, my collaborators and I examined the response of increasing water temperature on coregonine embryonic development. A collaborative cross-continent and cross-species approach was used to experimentally evaluate the responses of embryos to increasing incubation water temperatures. The effect of temperature on coregonines has been previously studied at local scales (John & Hasler

1956; Colby & Brooke 1973; Luczyński & Kirklewska 1984; Eckmann 1987; Karjalainen et al. 2015), but these studies are not comparable due to the absence of standardized methods (e.g., different incubation apparatuses, local water sources, water flow rates, bacterial and fungicide treatments, etc.), which can influence experimental results. In this chapter, standardized and reproducible experimental incubation methods were developed and tested to support the objective of implementing large-scale, comparative coregonine research and to provide a benchmark for future comparisons. Cisco from lakes Superior and Ontario (USA/Canada) and vendace and European whitefish from Lake Southern Konnevesi (Finland) were compared. I analyzed the temperature responses for embryo survival, incubation period, total length-at-hatch, and yolk-sac volume at hatching. A resultant manuscript was written and published in *Hydrobiologia*.

In Chapter 3, I tested the hypothesis that exposure to elevated light intensity due to less ice formation decreases cisco embryo survival and accelerates embryogenesis in the Great Lakes. I used the incubation methods developed in Chapter 2 and simulated three light treatments to mimic the *in situ* day-light intensities under 0-10 (high light), 40-60 (medium light), and 90-100% (low light) ice coverage throughout embryogenesis. Cisco from lakes Superior and Ontario were compared and the responses for embryo survival, incubation period, total length-at-hatch, and yolk-sac volume at hatching were analyzed. A resultant manuscript was written and published in the *Journal of Great Lakes Research*.

In Chapter 4, I studied how cisco embryo incubation temperatures influenced the survival and performance of hatching larvae from lakes Superior and Ontario. I reared the hatched larvae from Chapter 2 in a common environment. Sixty days post-hatch, larvae were exposed to a thermal challenge to explore the relationship between winter incubation temperatures and larval thermal tolerance. Larval cisco survival, absolute growth rates, and critical thermal limits were compared between lakes and across incubation temperatures. A resultant manuscript was written and in peer review with the *Journal of Great Lakes Research*.

In Chapter 5, my collaborators and I modelled the interactions between climatic-warming scenarios and changes in reproductive phenology of coregonine populations across North America and Europe. Using temperature-dependent embryo development models, I examined how three projected climate-forcing pathways (RCP 2.6, 4.5, and 8.5; IPCC, 2014) may change coregonine spawning times and period length, embryo development rates, and the time and period length of hatching. The predicted changes in reproductive phenology were compared for cisco from two populations in Lake Superior (Apostle Islands and Thunder Bay) and one from Lake Ontario, vendace from Lake Southern Konnevesi, and European whitefish in lakes Constance (Germany), Geneva (France), Bourget (France), and Annecy (France). A resultant manuscript is in preparation.

Overall, my research explored the influence temperature and ice conditions have on early-life stage coregonines and the predicted future impact warming may have on coregonine reproductive phenology. I explored multiple spatial scales, from localized

within the Great Lakes to cross-continent comparisons using field, laboratory, and modeling approaches. My research uncovered that coregonines are adapted to local environmental conditions. Based on these findings, I suggested ways that we might expect coregonine populations to respond to changing climates.

Climate change compounds the uncertainty of fisheries management. Projections estimate that up to one-third of species worldwide will go extinct by 2050 with no change in greenhouse gas emissions (IPCC 2014). These changes are likely to devastate cold-water lake fish communities and the ecosystem services they support. Climate-driven changes in habitat and fish communities may be inevitable for some lakes, but documenting known sources of uncertainty from published literature, ecological knowledge, and trait-based analyses is a critical component to assessing the specific future vulnerability of lake fish species. To this end, expanding conventional perspectives and thinking outside of the lake to explore novel approaches will improve coregonine restoration efforts.

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Table 1.1: Examples of *Coregonus spp.* life-history diversity.

Species	Geographic Range	Spawning Habitat	Spawning Time	Reproductive Strategy	Adult Feeding Habitat
<i>Coregonus artedii</i>	North America	Littoral and Sublittoral	Autumn and Spring	Lacustrine and Adfluvial	Nearshore pelagic
<i>Coregonus clupeaformis</i>	North America	Littoral	Autumn	Lacustrine and Adfluvial	Benthic
<i>Coregonus kiyi</i>	Laurentian Great Lakes	Deep benthic	Unknown	Lacustrine	Deep pelagic
<i>Coregonus sardinella</i>	Arctic Ocean basin	Littoral rivers	Autumn	Adfluvial	Brackish estuary
<i>Coregonus laurettae</i>	Alaskan Rivers and Coast	Littoral rivers	Late-summer	Adfluvial	Rivers and estuaries
<i>Coregonus albula</i>	Baltic and North Sea basins	Littoral and Sublittoral	Autumn and Spring	Lacustrine	Nearshore pelagic
<i>Coregonus lavaretus</i>	Europe and Asia	Littoral and Limnetic	Autumn	Lacustrine and Adfluvial	Benthic
<i>Coregonus fontanae</i>	Germany	Littoral	Spring	Lacustrine	Nearshore pelagic

## CHAPTER 2: INFLUENCE OF WARMING TEMPERATURES ON COREGONINE EMBRYOGENESIS WITHIN AND AMONG SPECIES

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## Abstract

The greatest known global response of lakes to climate change has been an increase in water temperatures. The responses of many lake fishes to warming water temperatures are projected to be inadequate to counter the speed and magnitude of climate change. We experimentally evaluated the responses of embryos from a group of cold, stenothermic fishes (Salmonidae Coregoninae) to increased incubation temperatures. Study groups included cisco (*Coregonus artedii*) from lakes Superior and Ontario (USA), and vendace (*C. albula*) and European whitefish (*C. lavaretus*) from Lake Southern Konnevesi (Finland). Embryos from artificial crossings were incubated at water temperatures of 2.0, 4.5, 7.0, and 9.0°C, and their responses were quantified for developmental and morphological traits. Embryo survival, incubation period, and length-at-hatch were inversely related to incubation temperature whereas yolk-sac volume increased with incubation temperature within study groups. However, varying magnitudes of responses among study groups suggested differential levels of developmental plasticity to climate change. Differential levels of parental effects indicate genetic diversity may enable all study groups to adapt to cope with some degree of changing environmental conditions. Our results suggest that the coregonines sampled within and among systems may have a wide range of embryo responses to warming incubation conditions.

## **Introduction**

Freshwater lakes are sensitive to climate change (Jenny et al. 2020; Woolway et al. 2020), and one of the greatest threats to lakes from climate change on a global scale is rising water temperatures (Austin & Colman 2007; O'Reilly et al. 2015; Maberly et al. 2020; Woolway et al. 2020). The greatest seasonal increase in water temperature of seasonally ice-covered lakes is projected to take place during the spring (Schindler et al. 1990; Winslow et al. 2017), concurrent with expected seasonal increases in air temperature during winter in the northern hemisphere (Christensen et al. 2007; Sharma et al. 2019). Such changes are likely to challenge aquatic organisms with life-history traits that include critical life stages during the winter-to-spring transition in these regions.

Warming spring water temperatures and increases in the length of the frost-free season can prolong annual growing seasons for aquatic organisms through warmer summers, longer and warmer autumns, and shorter ice-cover duration (Sharma et al. 2019; Sharma et al. 2020). Temperature is an abiotic master factor for aquatic ecosystems because water temperature directly affects the physical and chemical properties of water, and phenology, reproductive events, metabolic rates, growth, and survival of aquatic organisms (Fry 1964; Brett 1979; Gillooly et al. 2002; Brown et al. 2004; Ohlberger et al. 2007; Busch et al. 2012; Cline et al. 2013; Little et al. 2020). The responses of many lake organisms to climate-derived changes in lake ecology are projected to be inadequate to counter the speed and magnitude of climate change, leaving some species vulnerable to decline and extirpation (Hoffmann & Sgrò 2011). These pressures present challenges for biodiversity conservation and sustainability of ecosystem services. To navigate

challenges, a foundational understanding of the primary threats to aquatic ecosystems and organisms across a range of spatial scales from local to global is needed (Vörösmarty et al. 2010; Halpern et al. 2015; Langhans et al. 2019).

The effects of increasing temperature on lake fishes are predicted to lead to declines in cold-water species and increases in warm-water species (Comte et al. 2013; Hansen et al. 2017). Species that possess narrow optimal thermal ranges, live near their thermal limits, or have long development times at cold temperatures are at-risk under warming climate scenarios as temperature can have strong direct and indirect effects at early-life stages (Blaxter 1991; Pepin 1991; Ficke et al. 2007; Mari et al. 2016; Lim et al. 2017; Dahlke et al. 2020). Unlike their marine counterparts, most freshwater fishes are restricted to their lake system, where their ability to evade the effects of climate change is impeded due to the isolated nature of lakes (Ficke et al. 2007). The ability of lake fish populations living close to their upper thermal limits to respond either through physiological adaptation or physiological plasticity will be required if species are to persist under increasingly stressful thermal conditions (Somero 2010; Woolsey et al. 2015; Howells et al. 2016). Additionally, the amount of genetic variability within a population may constrain the ability to cope with environmentally-induced changes (*i.e.*, phenotypic plasticity; Schindler et al., 2010, 2015; Somero, 2010).

Freshwater whitefishes, Salmonidae Coregoninae (hereafter coregonines), are of great socio-economic value (Nyberg et al. 2001; Ebener et al. 2008; Vonlanthen et al. 2009; Vonlanthen et al. 2012; Lynch et al. 2015; Lynch et al. 2016), and are also considered to be critically sensitive to the effects of climate change because they are cold,

stenothermic fishes (Stockwell et al. 2009; Elliott & Bell 2011; Jeppesen et al. 2012; Isaak 2014; Jonsson & Jonsson 2014; Karjalainen et al. 2015; Karjalainen, Jokinen, et al. 2016). Coregonine fisheries worldwide have experienced population declines due to highly variable and weak year-class strengths (Nyberg et al. 2001; Vonlanthen et al. 2012; Anneville et al. 2015; Myers et al. 2015). In the 20th century, causes of decline included fishing and stocking practices (Anneville et al. 2015) and eutrophication causing poor incubation conditions (Müller 1992; Vonlanthen et al. 2012). Today, in the northern hemisphere, the trophic state of lakes and fisheries management practices are improving, but coregonines continue to be the focus of reintroduction, restoration, and conservation efforts in many lakes (Favé & Turgeon 2008; Zimmerman & Krueger 2009; Bronte et al. 2017). Reasons for declining recruitment are unknown, but climate change, increasing water temperatures, and habitat degradation are hypothesized as the main causal factors (Nyberg et al. 2001; Marjomäki et al. 2004; Jeppesen et al. 2012; Anneville et al. 2015; Karjalainen et al. 2015; Karjalainen, Jokinen, et al. 2016).

Coregonines generally spawn during late-autumn, embryos incubate over winter, and hatch in early- or late-spring (Stockwell et al. 2009; Karjalainen et al. 2015). The time between fertilization and hatching is inversely related to water temperature (Colby & Brooke 1970; Colby & Brooke 1973; Luczyński & Kirklewska 1984; Pauly & Pullin 1988; Karjalainen, Jokinen, et al. 2016). Rising spring water temperatures (*e.g.*, > 4°C) trigger hatching of autumn-spawned coregonine embryos (Häkkinen et al. 2002; Urpanen et al. 2005; Karjalainen et al. 2015). The length of the newly-hatched larvae is negatively correlated with the temperature of incubation (Colby & Brooke 1970; Colby & Brooke

1973; Luczyński & Kirklewska 1984; Karjalainen et al. 2015). The long period between spawning and hatching exposes coregonines to a variety of thermal conditions, potentially resulting in a wide range of environmentally-induced phenotypes or plastic responses (Karjalainen et al. 2015; Karjalainen, Jokinen, et al. 2016; Karjalainen, Urpanen, et al. 2016). Coregonines are known to be behaviorally and developmentally plastic (Muir et al. 2013) and some species (*e.g.*, vendace *Coregonus albula* and European whitefish *C. lavaretus*) can respond to short- and long-winter conditions within the limits of phenotypic plasticity and through genetic adaptive changes, such as different embryo developmental rates (Karjalainen et al. 2015; Karjalainen, Jokinen, et al. 2016).

Geographic variation is also important to consider with phenotypic plasticity. Many fishes in high-latitudes are adapted to relatively colder waters, extensive periods of ice cover, and strong seasonal daylight variations (Reist et al. 2006). Thus, high-latitude populations can show differential long-term adaptation to climates, compared to low-latitude population, across a latitudinal gradient (Conover & Present 1990; Yamahira & Conover 2002; Chavarie et al. 2010; Wilder et al. 2020). For example, a number of fishes have demonstrated an inverse relationship between length of the growing season and reproductive characteristics (*i.e.*, countergradient variation; Conover & Present, 1990; Conover & Schultz, 1995; Schultz et al., 1996, 1998; Billerbeck et al., 2000; Jonassen, 2000; Yamahira & Conover, 2002; Chavarie et al., 2010). Fishes at high latitudes experience lower temperatures overall and shorter growing seasons and should exhibit lower standard metabolic rates, growth rates, and smaller size-at-age than individuals at low latitudes (Reist et al. 2006; White et al. 2012). However, for cold-water stenothermic

fishes, water temperatures at low latitudes may exceed their optimal range for significant portions of the growing season, or the amount of optimal thermal habitat decrease, while water temperatures at high latitudes may remain near the optimum for maximal growth efficiency throughout the growing season (Conover & Schultz 1995). Because water temperature has a great influence on fish physiology and varies across latitudes, a wide range of adaptive responses by populations to increasing temperatures across latitudes is possible (Reist et al. 2006). However, in the absence of genetic information, phenotypic changes are difficult to distinguish as genetically based or the result of phenotypic plasticity (Merilä & Hendry 2014; Fox et al. 2019). Large-scale experimental studies across geographic regions can aid our understanding of the role of phenotypic plasticity relative to adaptive evolution by leveraging long-term adaptations to distinct geographic locations and environments (Hoffmann & Sgrò 2011; Merilä & Hendry 2014; Fox et al. 2019). Coregonines occur broadly across northern latitudes and are an ideal group to test how cold-water lake fishes may respond to climate-driven shifts in environmental variables, such as water temperature.

Our objective was to compare the reaction norms of coregonine embryos within and among species from multiple sampling locations across North America and Europe to a standardized thermal gradient during incubation. We hypothesized that coregonines have differential levels of phenotypic plasticity in developmental and morphological traits of embryos in response to warming winter incubation conditions based on putative adaptation to their local environments. We predicted coregonines that share the same

thermal environment respond similarly and geographically distinct groups with different thermal environments respond dissimilarly to increasing incubation temperatures.

## **Methods**

### *Study Species and Locations*

We used a cross-lake, cross-continent, cross-species approach to evaluate the responses and thermal tolerances of coregonine embryos to changing thermal regimes. Wild-caught populations of cisco (*C. artedii*) in Lake Superior (LS-Cisco; USA/Canada) and Lake Ontario (LO-Cisco; USA/Canada), and vendace (LK-Vendace) and European whitefish (LK-Whitefish) in Lake Southern Konnevesi (Finland; Figure 2.1) were sampled.

Cisco is one of the most widespread of the North American species of coregonines (Eshenroder et al. 2016) and were one of the most abundant fish in the Great Lakes (Yule et al. 2013). Cisco is found in north-central to eastern United States and throughout most of Canada, with the lower Great Lakes close to its southernmost extent (Scott & Crossman 1973). Cisco spawning is initiated when water temperatures decrease to 4-5°C in late-autumn (Pritchard 1931; Eshenroder et al. 2016) and occurs at different spawning depths. Spawning can occur at depths of 1-5 m in Lake Ontario (Pritchard 1931; Paufve 2019) and 10-64 m in Lake Superior (Dryer & Beil 1964; Paufve 2019). Experimental thermal optima for normal cisco embryo development is between 2 and 8°C (Colby & Brooke 1970; Brooke & Colby 1980). However, temperature data at historical spawning grounds indicate that *in-situ* incubations typically occur between 1 and 4°C, with Lake Ontario warmer than Lake Superior (Figure 2.2; unpublished data).

Optimal growth and upper lethal temperatures for cisco adults are estimated to be 18° and 26°C, respectively (Edsall & Colby 1970; McCormick et al. 1971; Jobling 1981).

Vendace and European whitefish are widely distributed in Northern Europe (Sipponen et al. 2006). Vendace spawning is initiated when water temperatures decrease to 6°C at the end of October in Lake Southern Konnevesi and lasts 2-3 weeks (Karjalainen & Marjomäki 2018). European whitefish spawn 2-3 weeks later in November when water temperatures decrease to 4-5°C (Karjalainen et al. 2015). Spawning of vendace occurs in the littoral and sublittoral zone of lakes and eggs dispersed widely at depths less than 20 m (Heikkilä et al. 2006; Karjalainen et al. 2021). Whitefish are known to spawn at shallower depths than vendace. Embryos are incubated at 1-2°C until the beginning of April, when water temperatures have gradually increased, and hatching peaks after ice-out at 4-6°C (Figure 2.2, Karjalainen et al., 2015). Although whitefish spawn later than vendace, their hatching occurs at the same time or slightly earlier than vendace (Karjalainen et al. 2015). Optimal growth and upper lethal temperatures for adults are estimated to be 18° and 27°C for immature vendace and 18° and 29°C for European whitefish, respectively (Tapaninen et al. 1998; Vielma et al. 2002; Siikavuopio et al. 2012).

#### *Adult Collections*

Adults were sampled using multi-mesh gillnets (51-89 mm stretched mesh) in Lake Superior (46.85°, -90.55°), trap nets in Lake Ontario (44.05°, -76.20°), and seines (vendace) and multi-mesh gillnets (European whitefish; 27-35 mm knot to knot mesh) in Lake Southern Konnevesi (62.58°, 26.58°). Adult field collections occurred during

coregonine spawning periods for Lake Ontario and Lake Superior. On Lake Southern Konnevesi, adults were collected prior to spawning and held in aquaculture pools with water fed directly from the lake until spawning was initiated. Demographic data (*e.g.*, total length, mass, and egg diameter) were collected on sampled adults. All sampling, fertilization, and experimental work for study groups on each continent were conducted at a single laboratory in North America (University of Vermont (UVM), USA) and Europe (University of Jyväskylä (JYU), Finland). Experiments were performed during the 2018-19 season in Finland and the 2019-20 season in the USA.

For clarity, our operational use of a study group is to represent a single species haphazardly sampled from a single location within a single lake (*e.g.*, cisco from the Apostle Islands region in Lake Superior). Our sampling efforts represent a single location within large lakes and likely do not capture all possible genetic variation within a species or population.

#### *Crossing Design and Fertilization*

Eggs and milt were stripped from 12 females and 16 males from each study group and artificially fertilized under a blocked, nested full-sib, half-sib fertilization design to create a maximum of 48 full-sibling families nested within half-siblings per group. The crossing design maximized the amount of genetic variation and minimized the potential loss of multiple families if a female or male produced poor quality gametes, for a given total number of families, compared to a full-factorial design. Adults used in the experiment were divided into three or four fertilization blocks. A single block consisted

of four males each paired to three females, where all offspring of a given female were full siblings. Fertilizations were performed block by block to ensure germ cell survival.

Approximately 200 eggs per female were fertilized with an equal amount of milt (5-15  $\mu$ l) from each male in the block. After the addition of milt, water was added to activate the germ cells and gently mixed for one minute. The embryos were rinsed with water 2-3 times until the water was clear. Temperature of the water used during all fertilizations was ca. 4°C. Reconstituted freshwater medium (International Organization For Standardization 6341, 2012) was used during fertilizations to standardize the chemical properties of the water used among study groups and between labs. Embryos were transported in coolers either by shipping overnight for Lake Superior or driven same-day for Lake Ontario. A temperature logger (HOBO<sup>®</sup> Water Temperature Pro v2) recorded air temperature inside the cooler during transport [Lake Superior: mean (SD) = 2.80°C (0.21); Lake Ontario: mean (SD) = 3.28°C (0.37)]. No embryo transport was required for Lake Southern Konnevesi. Fertilization success was determined by haphazardly taking 10 embryos from each family and assessing under microscopy within 72-hours post-fertilization (Oberlercher & Wanzenböck 2016). If fertilization was low (<30%), the family was removed from the experimental setup.

#### *Rearing Conditions*

Embryos from successfully fertilized families were individually distributed into 24-well cell culture microplates and incubated in 2 ml of reconstituted freshwater. Reconstituted freshwater was used during incubation to maintain sterility, prevent bacterial growth in the wells, and eliminate the need for fungicide treatments on the

embryos. A total of 36 embryos per family were used for Lake Southern Konnevesi species and 48 embryos per family for each of Lake Ontario and Lake Superior cisco. Families were randomly distributed across three or four microplates (*i.e.*, 12 eggs per family per microplate and two families per 24-well microplate). Microplates from each study group were incubated at target constant temperatures of 2.0 (coldest), 4.5 (cold), 7.0 (warm), and 9.0°C (warmest) and randomly placed in climate-controlled chambers at UVM (Memmert® IPP260Plus) and climate-controlled rooms at JYU (Huurre®). The range of experimental incubation temperature treatments was chosen to mimic *in-situ* mean temperatures and to exceed optimum embryonic development temperatures. Forced airflow was used in both the climate-controlled chambers and rooms to ensure equal air circulation around the microplates. All microplates were covered to minimize evaporation. Microplate orientation and position were rotated weekly to eliminate any temperature heterogeneity within the chambers and rooms. HOBO® TMCx-HD temperature probes were used at UVM to record water temperatures hourly in 50-ml beakers placed inside each climate chamber, while Escort iMini temperature loggers were used directly inside the well of a subset of microplates for each temperature treatment at JYU. Daily mean water temperatures were calculated. Incubations took place in the dark, with the exception of short (< 60 mins) maintenance periods. Microplates were checked weekly for dead eggs and the eye-up stage. During the hatch period, microplates were checked on a two-day cycle for newly hatched larvae. For cisco, all newly hatched larvae were photographed for developmental and morphological traits (Nikon® D5600 and Nikon® AF-S DX 18-55mm lens). Egg size, total length, and yolk-sac axes were

measured from images using Olympus® LCmicro. For Lake Southern Konnevesi, the larvae were preserved in ethanol at hatch and flushed and soak in distilled water for 15 min before measuring the total length and fresh mass under the microscope (Karjalainen 1992).

Mean water temperature during incubations was maintained near the target incubation temperature for the cold and warm treatments at each lab. Mean incubation water temperatures for the cold and warmest treatments were lower than the target incubation temperature at JYU, but not at UVM (Table 2.1).

#### *Developmental and Morphological Traits*

Embryo survival was estimated as the percent of embryos surviving between the eye-up and hatch stages to rule out unfertilized eggs which can bias survival estimates. Incubation period was assessed by two variables: the number of days from fertilization to hatching (days post-fertilization; DPF) and the sum of the degree-days (accumulated degree-days; ADD). Total length-at-hatch (mm) and yolk-sac volume (YSV; mm<sup>3</sup>) were measured from five individuals per family at, or as close as possible to, 50% hatching for each family. Yolk-sac volume was calculated assuming the shape of an ellipse (Blaxter & Hempel 1963):

$$YSV = \frac{\pi}{6} ab^2,$$

where a = length of the yolk sac (mm) and b = height of the yolk sac (mm).

#### *Statistical Analyses and Estimation of Variance Components*

Embryo survival was analyzed as a binomial response variable, and incubation period, length-at-hatch, and yolk-sac volume at hatching as continuous response

variables. Early embryo mortality and variable fertilization success induced from fertilization failure produced inequalities in the number of offspring among families. The sample size for incubation period is a function of embryo survival and subsequently resulted in an unbalanced design. All non-proportional data were checked visually for approximate normality using histograms and Q-Q plots before the analysis with parametric models. A cubic transformation was applied to LAH for cisco and a cubic root transformation was applied to DPF, ADD, and YSV to normalize the distributions. Therefore, binary data (*i.e.*, embryo survival) were analyzed with binomial generalized linear mixed-effects models (LMM) and transformed variables (*i.e.*, DPF, ADD, LAH, and YSV) were analyzed with restricted maximum likelihood LMMs with the *lme4* package v.1.1-26 (Bates et al. 2015). To eliminate any confounding effects between continents, cisco from lakes Superior and Ontario were analyzed independently from vendace and European Whitefish from Lake Southern Konnevesi. Population (for cisco only), species (for Lake Southern Konnevesi only), and incubation temperature were included as fixed effects and female, male, family (female and male combination), microplate, and fertilization block as random effects. Because embryos were raised independently, the replication unit in the statistical models is the individual embryo. Although incubation temperature was treated as a fixed variable based on our experimental design (*i.e.*, few treatment levels with high replication), we acknowledge that temperature is a continuous, independent variable in nature. All traits were examined for population or species, depending on the continent, and incubation temperature effects in addition to individual parental effects (female, male, and family effects), microplate,

fertilization block, and all possible interactions with backward, stepwise effect-selection using the *buildmer* package v.1.7.1 (Voeten 2020). The maximal model for each trait was selected by comparing a model including or lacking the term of interest to the reference model based on changes in log-likelihood, Akaike information criterion, Bayesian information criterion, and change in explained deviance. Significance values for the mixed-effects model parameters (*i.e.*, population, species, incubation temperature, interaction effects, and any random-effects selected) were determined using a likelihood ratio test between the maximal model and reduced models with the model parameter of interest removed (Myers et al. 1995; Luke 2017). All statistical tests used  $\alpha = 0.05$  to determine significance.

To allow for interspecific comparisons, the response to temperature for each trait was standardized to the optimal temperature for each study group. Based on literature data (cf. above), the coldest incubation temperature treatment (2.0°C and 2.2°C; Table 2.1) was assumed to be the optimal incubation temperature. For each trait, the within-family mean was calculated for each temperature treatment and the percent change from the optimal temperature estimated. Standard error was calculated as the among-family variation in percent change.

The phenotypic variance components were partitioned into random effects for female, male, female x male, and unexplained or random residual variance components using mixed-effects models with the *fullfact* package v.1.3 (Houde & Pitcher 2016) for each study group and incubation temperature treatment. Negative variance components were treated as zero (Neff & Pitcher 2005). The percent of total phenotypic variation was

used to calculate the Pearson correlation coefficient between each variance component and the increase in incubation temperature for each study group. A threshold of  $\pm 0.7$  (*i.e.*, an  $R^2$  of 0.49) was used to categorize correlations either positive or negative, with all values in between as no correlation. European whitefish from Lake Southern Konnevesi were removed from this analysis due to a low embryo survival and a low number of families.

All analyses were performed in R version 4.0.3 (R Core Team 2021).

## **Results**

### *Spawning Adults*

Total lengths and fresh mass of spawning adults used for gamete collection varied widely among study groups (Table 2.2). LK-Vendace were notably smaller than all other study groups. The remaining study groups varied less in size, but LK-Whitefish were smaller than LS-Cisco and LO-Cisco.

The LK-Vendace females had the smallest egg diameters and LO-Cisco females had the largest egg diameters among the study groups (Table 2.3). LK-Whitefish and LS-Cisco egg diameters were similar (Table 2.3).

### *Developmental and Morphological Traits and Variance Components*

All cisco traits had significant interaction effects between population and incubation temperature (maximum  $P < 0.001$ ; Tables 2.4 and 2.5). All vendace and European whitefish traits had significant interaction effects between species and incubation temperature (maximum  $P = 0.002$ ; Tables 2.4 and 2.5). The interaction effects precluded any interpretation of main effects but did suggest different norms of reaction

for the model groups. Below we describe the interaction effects. All random effects (*i.e.*, female, male, and female x male) were significant (maximum  $P = 0.038$ ) except male for LAH and female x male for LAH and YSV in cisco (Tables 2.4 and 2.5). All statistical model results can be found in Tables 2.4 and 2.5.

### Embryo Survival

Embryo survival was highest among all study groups at the coldest temperature and lowest at the warmest temperature (Figure 2.3). The effect of temperature for cisco depended on population because embryo survival was higher for LO-Cisco (99.3%) than LS-Cisco (80.0%) at the coldest temperature but not different between populations (difference  $< 0.1\%$ ) at the warmest temperature (Figure 2.3). For Lake Southern Konnevesi, the effect of temperature depended on species because the difference in embryo survival between LK-Vendace and LK-Whitefish was less pronounced at the coldest temperature (29.0%) than at the warmest temperature (50.5%; Figure 2.3). LK-Vendace and LK-Whitefish embryo survival had a differential temperature response as LK-Whitefish had a greater decrease (74.4%) than LK-Vendace (17.7%) from the coldest to warmest incubation temperatures. LK-Whitefish had the strongest, decreasing response to increasing incubation temperatures compared to all other study groups (Figure 2.3).

In the phenotypic variance component analysis, the residual error was the largest component of phenotypic variation in embryo survival (means  $> 55.2\%$ ) for all study groups (Figure 2.4, Table A.1). The mean female variance had the highest percentage, excluding error, of the phenotypic variation in embryo survival for LK-Vendace (17.4%), LS-Cisco (24.1%), and LO-Cisco (19.9%; Figure 2.4, Table A.1). The female variance

component correlations for embryo survival had either negative or no correlations to increasing temperature; however, male and error variances had positive and no correlations suggesting that as the female component decreases at higher temperatures the importance of the male component and error increases (Table 2.6).

*Incubation Period (days post-fertilization)*

The number of days post-fertilization to hatching was highest for all study groups at the coldest temperature and decreased as temperature increased (Figure 2.3). For cisco, DPF was higher for LO-Cisco (179.2 days) than LS-Cisco (154.3 days) at the coldest temperature and the difference between populations was less pronounced at the warmest temperature (difference = 5.0 days; Figure 2.3). For Lake Southern Konnevesi, the effect of temperature depended on species because the difference in DPF between LK-Vendace and LK-Whitefish was less pronounced at the coldest temperature (8.9 days) than at warmest temperature (27.3 days; Figure 2.3). All study groups had similar responses to temperature, with between 54.2 to 68.3% decreases in DPF from the coldest to warmest treatments. However, LS-Cisco, LO-Cisco, and LK-Whitefish had a greater decrease in DPF (66.1, 68.3, 65.3%, respectively), than LK-Vendace (54.2%; Figure 2.3).

In the phenotypic variance component analysis, the residual error was the largest component of phenotypic variation in DPF (means >60.8%) for LK-Vendace and LS-Cisco (Figure 2.4, Table A.2). The mean female variance was the largest phenotypic variation component in DPF for LO-Cisco (47.1%). LK-Vendace and LS-Cisco had similar mean female variances for DPF across all temperatures, with 28.1 and 21.0%,

respectively (Figure 2.4, Table A.2). The DPF correlations for female effect had a negative response to temperature for LS-Cisco and LO-Cisco (Table 2.6).

*Incubation Period (accumulated degree-days)*

Accumulated degree-days were highest for all study groups at 6.9°C (Figure 2.3). The effect of temperature for cisco depended on population because ADD was higher for LO-Cisco (531.9 and 547.7 ADD) than LS-Cisco (461.0 and 492.5 ADD) at the cold and warm temperatures, respectively, and the differences between populations were less pronounced at the coldest and warmest temperatures (differences = 49.2 and 41.3 ADD, respectively; Figure 2.3). LS-Cisco and LO-Cisco ADD responded similarly to increasing incubation temperature. For Lake Southern Konnevesi, the effect of temperature depended on species because the difference in ADD between LK-Vendace and LK-Whitefish was less pronounced at the coldest temperature (7.7 ADD) than at the warm temperature (198.1 ADD; Figure 2.3). LK-Vendace and LK-Whitefish ADD had a differential temperature response as LK-Vendace had a greater increase (198.4%) than LK-Whitefish (159.4%) from the coldest to warm treatment. LK-Vendace had the strongest, increasing response to increasing incubation temperatures compared to all other study groups (Figure 2.3).

In the phenotypic variance component analysis and correlations, ADD had a similar response as DPF among all study groups as the data only had a different temperature scaling factor (Figure 2.4, Tables A.3 and 2.6).

### Length-at-Hatch

All study groups had a common, decreasing response in LAH as temperature increased (Figure 2.5). For cisco, LAH was higher for LO-Cisco (11.32 and 9.75 mm) than LS-Cisco (10.21 and 8.68 mm) at the coldest and warmest temperatures, respectively, and the difference between populations was less pronounced at the cold and warm temperatures (differences = 0.99 and 0.90 mm, respectively; Figure 2.5). LS-Cisco and LO-Cisco responded to increasing incubation temperature with a 15.9 and 13.8% respective decrease in LAH from the coldest to warmest treatments. For Lake Southern Konnevesi, the effect of temperature depended on species because the difference in LAH between LK-Vendace and LK-Whitefish was more pronounced at the cold and warm temperatures (2.73 and 2.72 mm, respectively) than at the coldest and warmest temperatures (2.68 and 2.61 mm, respectively; Figure 2.5). LK-Vendace and LK-Whitefish each responded similarly to temperature with a 9.0 and 9.2% respective decrease in LAH from the coldest to warmest treatments. LS-Cisco and LO-Cisco LAH had a stronger, decreasing response to increasing incubation temperatures than LK-Vendace and LK-Whitefish (Figure 2.5).

In the phenotypic variance component analysis, the residual error was the largest component of phenotypic variation in LAH (means >49.2%) for all study groups (Figure 2.4, Table A.4). The mean female variance had the highest percentage, excluding error, of the phenotypic variation in LAH for LK-Vendace (40.6%), LS-Cisco (38.2%), and LO-Cisco (17.1%; Figure 2.4, Table A.4). The LAH correlations for each study group

had a similar response to temperature with negative or no female and male correlations and positive or no female x male correlations (Table 2.6).

### Yolk-sac Volume

Yolk-sac volume was highest for all study groups at 9.0°C and decreased as temperature decreased (Figure 2.5). For cisco, the difference in YSV was similar between populations at the warmest incubation temperature (0.04 mm<sup>3</sup>) but diverged as incubation temperature decreased; YSV in LO-Cisco (0.40 mm<sup>3</sup>) was smaller than LS-Cisco (0.64 mm<sup>3</sup>) at the coldest temperature (Figure 2.5). Yolk-sac volume in LS-Cisco and LO-Cisco responded differently to incubation temperature, with a 203.6 and 311.0% respective increase from the coldest to warmest treatment. For Lake Southern Konnevesi, the effect of temperature depended on species because the difference in YSV between LK-Vendace and LK-Whitefish was less pronounced at the coldest temperature (0.20 mm<sup>3</sup>) than at the warmest temperature (1.07 mm<sup>3</sup>; Figure 2.5). LK-Vendace and LK-Whitefish had the strongest response to temperature with an increase in YSV of 445.0 and 536.6% from the coldest to warmest treatment, respectively. LK-Vendace and LK-Whitefish had a stronger, increasing response to increasing incubation temperatures in YSV than LS-Cisco and LO-Cisco (Figure 2.5).

In the phenotypic variance component analysis, the residual error was the largest component of phenotypic variation in YSV (means >53.9%) for all study groups (Figure 2.4, Table A.5). The mean YSV female variance was the highest percentage, excluding error, of the phenotypic variation for LK-Vendace (23.9%), LS-Cisco (20.5%), and LO-Cisco (23.9%; Figure 2.4, Table A.5). The YSV correlations for female, female x male,

and error variance components had differential responses to temperature with positive female, positive female x male, and negative error correlations for LK-Vendace, while LS-Cisco had inverse correlations to LK-Vendace (Table 2.6). All LO-Cisco variance components had no correlation to temperature (Table 2.6).

## **Discussion**

Our incubation experiments demonstrated both similar and dissimilar reaction norms to temperature for developmental and morphological traits in coregonines. First, we found different responses to temperature in embryo survival within and among study groups. Second, incubation periods (both DPF and ADD) responded similarly to increasing temperature (negative response for DPF and positive response for ADD) among study groups, however, LK-Vendace had the strongest response and longest incubations across all temperatures. Third, all study groups had similar negative responses to temperature for LAH and positive responses in YSV, with the strongest responses for LAH in LS-Cisco and LO-Cisco and for YSV in LK-Vendace and LK-Whitefish. Lastly, differential levels of parental effects were found within and among study groups and traits.

Embryo survival had an overall negative correlation with increasing temperature among all study groups. However, cisco and vendace had different levels of response to temperature compared to European whitefish. LK-Whitefish embryo survival had the strongest, negative response to temperature (74.4% survival loss) and all other study groups were impacted less (< 26% survival loss) by increasing temperatures.

Temperature is a strong driver of coregonine embryo development (Karjalainen et al.

2015) and survival (Colby & Brooke 1970; Brooke & Colby 1980; Luczyński & Kirklewska 1984) but study groups showed different levels of sensitivity to increased incubation temperatures reflecting specific physiological adaptations.

Additionally, our experiment, temperature aside, provided near-optimal incubation conditions to individually reared embryos and these conditions are idealized compared to what occurs in the wild. For instance, embryos in the wild are deposited on the substratum and are exposed to deposited sediment that can impact survival (Müller 1992). Interaction between temperature and sediments are likely, and temperature increases may act as a catalyzer of embryo sensitivity to sediment stress (Mari et al. 2016; Mari et al. 2021). Even though temperature did negatively impact embryo survival in our experiment, the effect of temperature in the wild, in combination with other factors, could be even stronger. Similarly, both study groups from North America required transportation, which could have had negative effects on embryo survival. Lake Superior had a greater transportation distance and time than Lake Ontario, which could explain some of the difference observed in embryo survival between the two study groups. Lake Ontario embryos had > 99% survival at optimal temperatures which suggests that transportation did not impact them.

The longer incubation periods from LK-Vendace and LK-Whitefish and strong response to increasing temperatures, even at the warmest incubation temperatures, support previous findings that vendace and European whitefish from Lake Southern Konnevesi have a high degree of developmental flexibility (Karjalainen et al. 2015). The different response between vendace and European whitefish was likely due to species-

specific differences (Karjalainen et al. 2015) and ecotypes (*i.e.*, benthic versus pelagic; Mcphee et al., 2012). Additionally, the different magnitude of temperature responses among all study groups suggests a differential level of developmental plasticity to increasing incubation temperatures among species and locations. Long, relatively cold incubations may require a shorter period of spring warming for individuals to initiate hatching, while short, relatively warm incubations may require a longer period of warmer spring conditions to hatch (Karjalainen et al. 2015). If winter water temperatures rise as embryos incubate, the ability to match optimal spring nursery conditions may be weakened (Cushing 1990; Karjalainen et al. 2015; Myers et al. 2015). Populations that are more resilient to increasing or variable winter incubation temperatures may have a better opportunity to regulate ontogeny and adjust the time of hatching.

Fish spawning strategies are variable, ranging in frequency from daily to once in a lifetime and in timing from the same time each year to across all seasons (McBride et al. 2015). For many species, spawning strategies and breeding patterns are constrained by the adult body condition, gonadogenesis, and the environment (Jørgensen et al. 2006; van Damme et al. 2009; Muir et al. 2014; McBride et al. 2015). In this context, the short duration of cisco embryo incubation periods when exposed to high temperatures was notable. High-latitude populations typically spawn earlier in autumn and may have the opportunity to delay spawning later into the season, while still providing an adequate incubation period for embryo development, if water temperatures continue to rise and do not inhibit ovulation as a result of climate change. However, low-latitude coregonine populations already spawn in late-autumn and early-winter (Stockwell et al. 2009;

Eshenroder et al. 2016), which begs the question: do low-latitude populations have capacity to spawn later in the winter if temperatures continue to rise? Winter spawning may lead to less vulnerability to contemporary climate change. For instance, Atlantic herring (*Clupea harengus*) have both autumn- and winter-spawning stocks in the North Sea that share the same summer feeding grounds and start oocyte development at the same time (van Damme et al. 2009). Similarly, coregonines can exhibit varying spawning strategies.

Sympatric coregonine species with autumn, winter, and spring-spawning stocks co-occur in several northern- and central-Eurasian lakes (Eronen & Lahti 1988; Schulz & Freyhof 2003; Schulz et al. 2006; Ohlberger et al. 2008) and allopatric spring-spawning stocks of cisco are found in Lac des Écorces (southwestern Quebec; Pariseau et al., 1983; Hénault & Fortin, 1989, 1991). Winter and spring spawners continue oocyte development through autumn which results in a lower number of larger eggs compared to the autumn-spawning stocks (Eronen & Lahti 1988; Hénault & Fortin 1991). Oocyte development is driven by body energy content, and winter- and spring-spawning stocks may give iteroparous females the chance to mitigate the disproportionate energy demand toward somatic growth during the summer when metabolic demands are higher. Consequently, changes in the environment and the condition of an individual spawning adult could affect future coregonine spawning strategies. Our results suggest that the cisco embryos examined may not have the developmental plasticity to mitigate the effects of increased water temperatures on incubation period. In this context, adjusting the time of spawning may be a more efficient long-term life-history strategy than the embryos adapting to

increased temperatures. Research on the reproductive plasticity of coregonine adults (*e.g.*, changes to fecundity of females and size of eggs from temperature) in the face of climate change is a logical next step.

Lake morphology is also important to consider for the question of a winter- or spring-spawning adaptation; deeper lakes could sufficiently provide cold thermal refuges at greater depths if suitable spawning habitat is available and level of oxygen sufficient (Jane et al. 2020). Spring-spawning ciscos in Lac des Écorces, where a 4°C summer stratum does not exist, initiate spawning when spring water temperatures reach 6°C at depths ranging from 20-30 m (Hénault & Fortin 1989; Hénault & Fortin 1991). This strategy of spawning in deeper, colder water allows for normal embryogenesis throughout the summer to mitigate high water temperatures during the summer period at shallow depths. Model projections of suitable thermal and oxythermal habitat for cisco indicate deeper and less eutrophic lakes will likely provide the best cold-water habitat as water temperatures and land uses change (Jacobson et al. 2010; Herb et al. 2014; Schmitt et al. 2020). While deep lakes may possess acceptable thermal refugia for coregonines, access to and requirements for suitable spawning and incubation habitat is unknown for most populations.

In addition to lower survival and shorter incubations as temperature increases, we also found both similar and different responses to temperature in morphological traits (*i.e.*, length-at-hatch and yolk-sac volume) among study groups. The dissimilarity in morphological traits among study groups is likely related to different egg sizes at fertilization. Smaller eggs will produce smaller larvae, requiring a lower growth and

development rate and less demand on maternal yolk than larger eggs. The demand for yolk and egg size are positively related and temperature during embryogenesis is positively related to metabolic rate (Hodson & Blunt 1986; Kamler 2008). In all groups, LAH slightly decreases with increasing temperatures. In LK-Vendace and LK-Whitefish, however, YSV increases more strongly with temperature, than in cisco. This suggests a higher yolk conversion efficiency across all temperatures in LK-Vendace and LK-Whitefish than in cisco. All study groups had a decrease in YSV with time as basal metabolism consumed yolk as a function of the length of incubation. Regardless of the mode, our results suggest a synergistic relationship among species, location, egg size, incubation period, and incubation temperature in determining the phenotype of LAH and YSV.

The trade-off between LAH and YSV is well documented in larval fish physiology (Blaxter 1991). Climate change impacts may only exacerbate the importance of each morphological trait in determining either a match or mismatch between larval coregonines and their zooplankton prey. While our experiments used constant incubation temperatures due to logistical constraints, the impact different spring warming rates can have on the time of hatching and the size of larvae should not be ignored. Lake Southern Konnevesi vendace and European whitefish previously exhibited flexibility in embryo development rates and feeding windows under different warming scenarios (Karjalainen et al. 2015). Such complex responses challenge our ability to predict the downstream impacts changing autumn, winter, and spring water temperatures may have on embryo and larval phenotypic plasticity.

Traits of embryos depend not only on species, population, and incubation temperature but also on parental and transgenerational effects (Blaxter & Hempel 1963; Blaxter 1991; Kekäläinen et al. 2018). Our results suggest that both female and male effects controlled a portion of early-stage offspring trait phenotypes in coregonines. The variability in phenotypes induced by parental effects can provide more flexibility for a population to cope with changing inter-annual environmental conditions, prevent full year-class failure, and ensure population persistence (Wright & Trippel 2009; Oomen & Hutchings 2015; Karjalainen, Jokinen, et al. 2016). In fishes, the female effect is usually more pronounced than male and female x male interaction effects, and is stronger in traits directly related to egg size (Nagler et al. 2000; Kennedy et al. 2007; Huuskonen et al. 2011), and our results support this conclusion. Residual error estimates, however, remained high. Intersexual selection and mate pairing has been proposed as an important component affecting coregonine offspring fitness (Wedekind et al. 2008; Huuskonen et al. 2011; Karjalainen & Marjomäki 2018), and may play a role in conserving natural biodiversity within populations (Anneville et al. 2015). The long-term stability of commercially exploited stocks, which can experience fisheries-induced evolution, has been linked to population diversity (Schindler et al. 2010; Freshwater et al. 2019). Spawning stocks that comprise individuals of variable sizes and ages (*e.g.*, portfolio effect; Schindler et al., 2010) may contribute differently to spawning, offspring performance, and recruitment (Luck et al. 2003; Figge 2004), and are likely an important consideration as the rapid rate of climate change adds additional stressors on populations.

The methods we used provide reproducible experimental conditions (*e.g.*, uniform water source between laboratories, no moving water, minimal embryo disturbance, etc.) and standardized results that can be compared to future experiments that examine temperature responses across a wider range of populations. Additionally, efforts to include more northerly populations of cisco from Canada were thwarted due to restrictions on transport of live embryos across an international border. This further highlights the importance of the standardized experimental methods we used to allow for future large-scale, cross-laboratory experiments. However, our results do suggest that some form of latitudinal variation is likely present and promote fruitful opportunities for future large-scale experimental research on coregonines and other cold, stenothermic fishes.

Additionally, interpreting the impacts of parental responses within an environmental context continues to be important to determine how parental effects may mitigate species' responses to rapid climate change. The existence of varying parental responses raises questions concerning possible causal mechanisms. Genomic studies will be needed to better understand what is genetically impacted by increasing temperatures, how it is impacted, and when during development (*i.e.*, when is temperature most critical; Narum et al., 2013; Chen et al., 2018). A mechanistic understanding of thermal response from populations across latitudes will be essential to predict the vulnerability of species and populations to climate change. Furthermore, incorporating phylogenetic contrasts would highlight the shared phylogenetic history and genetic architecture among our study groups and aid future comparative studies examining phenotypic traits across species and

genera (Garland et al. 2005). This study does contain species from the same genus, but species are either reproductively isolated on different continents (*i.e.*, cisco and vendace) or are distinct ecotypes (*i.e.*, vendace and European whitefish). Moreover, stocking practices are important to consider, including supportive breeding, and may affect the adaptive potential of populations through an artificial selection process (Ford 2002; Christie et al. 2012; Anneville et al. 2015) and their ability to respond to environmental changes.

### **Conclusion**

Water temperature is fundamental in regulating fish physiology, and environmental variation during development can play a large role in generating variability in offspring through phenotypic plasticity (Little et al. 2020). How coregonines respond during the critical embryonic stage is important to determine whether the capacity to respond to climate change and the projected increases in their incubation temperatures exists. Knowing how populations have adapted historically to environmental variability will help us understand the range of possible responses to climate change and assist managers to keep coregonines out of hot water.

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Table 2.1: Mean (SD) water temperatures during embryo incubations at the University of Vermont (UVM) and University of Jyväskylä (JYU).

Laboratory	Incubation Temperature Treatment (°C)			
	2.0 Coldest	4.5 Cold	7.0 Warm	9.0 Warmest
UVM	2.0 (0.5)	4.4 (0.2)	6.9 (0.2)	8.9 (0.3)
JYU	2.2 (1.5)	4.0 (0.7)	6.9 (0.5)	8.0 (0.6)

Table 2.2: Mean (SD) total length (TL) and fresh mass (FM) of the female and males from Lake Southern Konnevesi [LK-Vendace (*Coregonus albula*) and LK-Whitefish (*C. lavaretus*)], Lake Superior [LS-Cisco (*C. artedi*)], and Lake Ontario (LO-Cisco).

Sex	LK-Vendace		LK-Whitefish		LS-Cisco		LO-Cisco	
	TL (mm)	FM (g)	TL (mm)	FM (g)	TL (mm)	FM (g)	TL (mm)	FM (g)
Female	144.67 (16.51)	18.36 (5.95)	256.57 (11.63)	117.00 (19.16)	428.92 (44.40)	676.02 (181.51)	380.33 (24.18)	567.59 (122.89)
Male	140.83 (9.22)	13.85 (2.27)	285.75 (40.86)	171.34 (87.22)	400.25 (34.35)	523.82 (134.65)	366.56 (25.30)	443.29 (103.16)

Table 2.3: Mean (SD) egg diameter of females with the number of eggs measured (N) from Lake Southern Konnevesi [LK-Vendace (*Coregonus albula*) and LK-Whitefish (*C. lavaretus*)], Lake Superior [LS-Cisco (*C. artedi*)], and Lake Ontario (LO-Cisco).

Population	Egg Diameter (mm)	N
LK-Vendace	1.58 (0.11)	273
LK-Whitefish	2.13 (0.12)	70
LS-Cisco	2.14 (0.12)	140
LO-Cisco	2.30 (0.08)	240

Table 2.4: Likelihood ratio test output for each model selected for embryo survival and incubation period [number of days post-fertilization (DPF) and accumulated degree days (°C; ADD)] from lakes Superior and Ontario cisco (*Coregonus artedii*) and Lake Southern Konnevesi vendace (*C. albula*) and European whitefish (*C. lavaretus*). The full model that was selected is bolded for each trait and species.

Trait	Species	Model	Effect Tested	df	$\chi^2$	p-value	
Embryo Survival	Cisco	<b>t + pop + t:pop + family + female</b>					
		pop + family + female	t	3	443.54	< 0.001	
		t + family + female	pop	1	600.61	< 0.001	
		t + pop + family + female	t:pop	3	198.56	< 0.001	
		t + pop + t:pop + female	family	1	181.47	< 0.001	
		t + pop + t:pop + family	female	1	23.36	< 0.001	
	Vendace & European Whitefish	<b>t + sp + t:sp + family + female</b>					
		sp + family + female	t	3	223.54	< 0.001	
		t + family + female	sp	1	993.43	< 0.001	
		t + sp + family + female	t:sp	3	52.94	< 0.001	
		t + sp + t:sp + female	family	1	1042.9	< 0.001	
		t + sp + t:sp + family	female	1	1015.8	< 0.001	
	Incubation Period (DPF)	Cisco	<b>t + pop + t:pop + family + female + male</b>				
			pop + family + female + male	t	3	31,183.13	< 0.001
t + family + female + male			pop	1	3,651.86	< 0.001	
t + pop + family + female + male			t:pop	3	315.04	< 0.001	
t + pop + t:pop + female + male			family	1	58.62	< 0.001	
t + pop + t:pop + family + male			female	1	65.04	< 0.001	
Vendace & European Whitefish		<b>t + sp + t:sp + family + female + male</b>					
		sp + family + female + male	t	3	7,178.37	< 0.001	
		t + family + female + male	sp	1	904.95	< 0.001	
		t + sp + family + female + male	t:sp	3	353.67	< 0.001	
		t + sp + t:sp + female + male	family	1	13.55	< 0.001	
		t + sp + t:sp + family + male	female	1	36.07	< 0.001	
Cisco		<b>t + pop + t:pop + family + female + male</b>					
		pop + family + female + male	t	3	15,519.48	< 0.001	
	t + family + female + male	pop	1	3,586.18	< 0.001		
	t + pop + family + female + male	t:pop	3	137.36	< 0.001		
	t + pop + t:pop + female + male	family	1	54.58	< 0.001		
	t + pop + t:pop + family + male	female	1	63.20	< 0.001		

	t + pop + t:pop + family + female	male	1	15.34	< 0.001
Vendace & European Whitefish	<b>t + sp + t:sp + family + female + male</b>				
	sp + family + female + male	t	3	3,571.72	< 0.001
	t + family + female + male	sp	1	763.19	< 0.001
	t + sp + family + female + male	t:sp	3	466.23	< 0.001
	t + sp + t:sp + female + male	family	1	12.70	< 0.001
	t + sp + t:sp + family + male	female	1	36.79	< 0.001
	t + sp + t:sp + family + female	male	1	4.33	0.038

t indicates temperature, pop indicates population, and sp indicates species

Table 2.5: Likelihood ratio test output for each model selected for length-at-hatch (mm) and yolk-sac volume (mm<sup>3</sup>) from lakes Superior and Ontario cisco (*Coregonus artedi*), Lake Southern Konnevesi vendace (*C. albula*), and Lake Southern Konnevesi European whitefish (*C. lavaretus*). The full model that was selected is bolded for each trait and species.

Trait	Species	Model	Effect Tested	df	$\chi^2$	p-value
Length-at-Hatch	Cisco	<b>t + pop + t:pop + female</b>				
		pop + female	t	3	886.79	< 0.001
		t + female	pop	1	628.15	< 0.001
		t + pop + female	t:pop	3	19.03	< 0.001
		t + pop + t:pop	female	1	161.40	< 0.001
	Vendace & European Whitefish	<b>t + sp + t:sp + family + female</b>				
		sp + family + female	t	3	467.20	< 0.001
		t + family + female	sp	1	2091.33	< 0.001
		t + sp + family + female	t:sp	3	14.49	0.002
		t + sp + t:sp + female	family	1	13.83	< 0.001
		t + sp + t:sp + family	female	1	48.81	< 0.001
Yolk-sac Volume	Cisco	<b>t + pop + t:pop + female</b>				
		pop + female	t	3	1,163.87	< 0.001
		t + female	pop	1	246.56	< 0.001
		t + pop + female	t:pop	3	99.25	< 0.001
		t + pop + t:pop	female	1	410.42	< 0.001
	Vendace & European Whitefish	<b>t + sp + t:sp + family + female + male</b>				
		sp + family + female	t	3	980.02	< 0.001
		t + family + female	sp	1	805.34	< 0.001
		t + sp + family + female	t:sp	3	107.58	< 0.001
		t + sp + t:sp + female	family	1	33.33	< 0.001
		t + sp + t:sp + family	female	1	6.96	0.008

t indicates temperature and pop indicates population.

Table 2.6: Phenotypic variation component correlation directions from increasing incubation temperature for embryo survival (%), incubation period (number of days post-fertilization; DPF), incubation period (accumulated degree-days; ADD), length-at-hatch (mm), and yolk-sac volume (mm<sup>3</sup>) from Lake Southern Konnevesi vendace [LK-Vendace (*Coregonus albula*)], Lake Superior cisco [LS-Cisco (*C. artedi*)], and Lake Ontario cisco (LO-Cisco).

Trait	Study Group	Correlation Direction			
		Female	Male	Female:Male	Error
Embryo Survival	LK-Vendace	-	+	0	+
	LS-Cisco	-	0	0	0
	LO-Cisco	0	+	0	+
Incubation Period (DPF)	LK-Vendace	0	0	+	0
	LS-Cisco	-	0	0	0
	LO-Cisco	-	0	0	+
Incubation Period (ADD)	LK-Vendace	0	-	+	0
	LS-Cisco	-	0	0	0
	LO-Cisco	-	-	0	+
Length-at-Hatch	LK-Vendace	0	-	+	0
	LS-Cisco	-	0	0	0
	LO-Cisco	-	0	+	0
Yolk-sac Volume	LK-Vendace	+	0	+	-
	LS-Cisco	-	+	-	+
	LO-Cisco	0	0	0	0

- indicates a negative correlation, + indicates a positive correlation, and 0 indicates no correlation.

Figure 2.1: Map showing the location of each lake (LS = Lake Superior; LO = Lake Ontario; LK = Lake Southern Konnevesi) sampled in North America (A) and Europe (B).

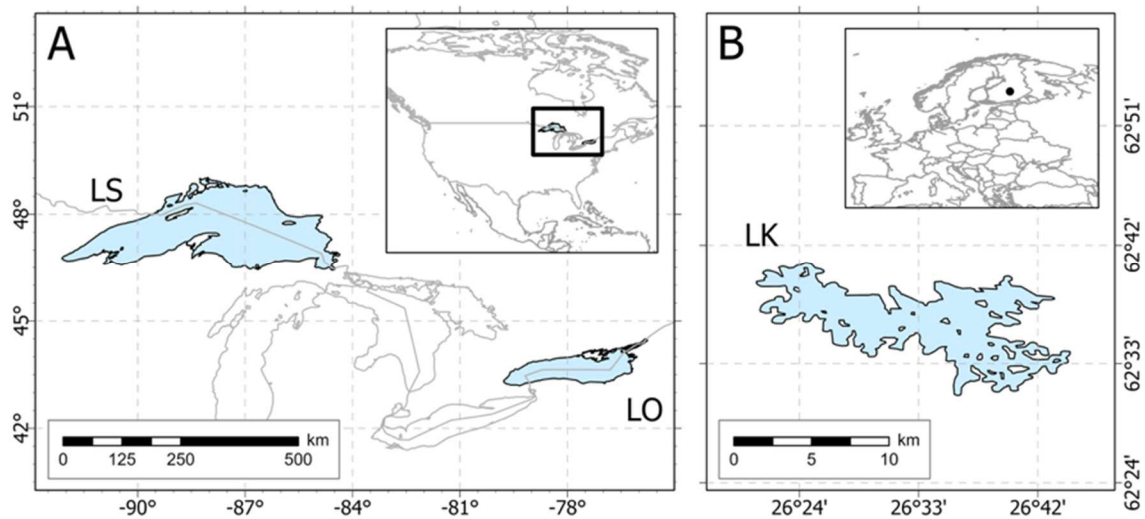


Figure 2.2: Winter water temperatures from Lake Southern Konnevesi, Lake Superior, and Lake Ontario. Lake Southern Konnevesi and Lake Superior data were recorded using *in-situ* sensors on the lakebed (10-m deep). Lake Ontario data was recorded using remote sensing sea surface temperatures. X indicates *ca.* spawning and O indicates *ca.* hatching. The earlier spawning (X) in Lake Southern Konnevesi indicates vendace (*Coregonus albula*) and latter for European whitefish (*C. lavaretus*).

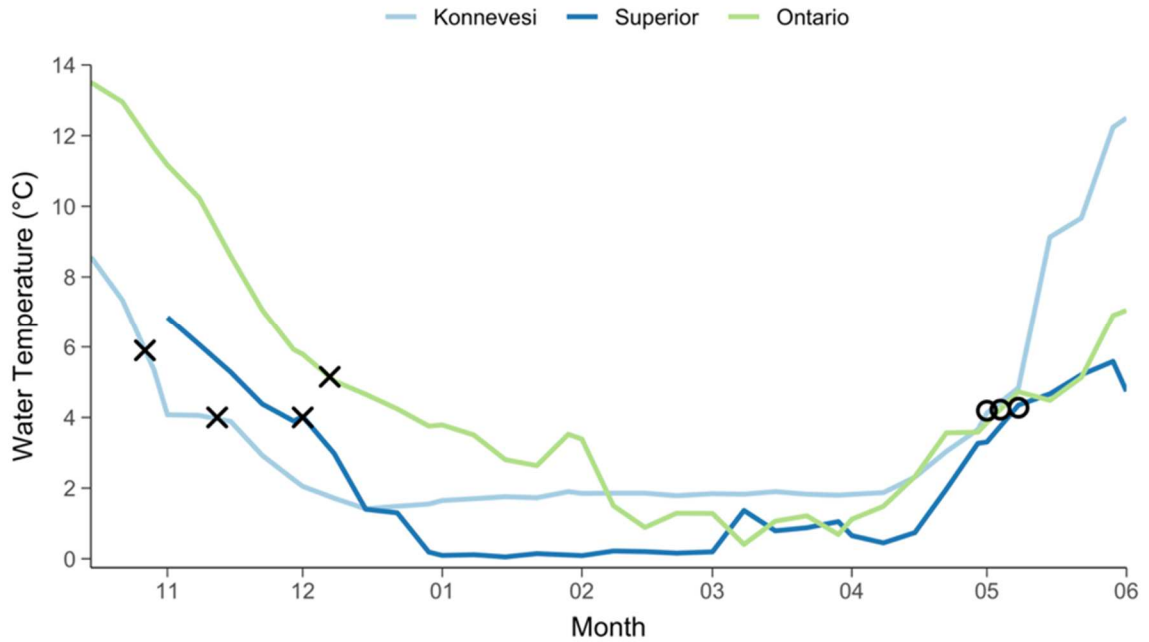


Figure 2.3: Mean embryo survival (%) and incubation period [number of days post-fertilization (DPF) and accumulated degree days ( $^{\circ}\text{C}$ ; ADD)] at each incubation temperature ( $^{\circ}\text{C}$ ; left) and standardized temperature responses within each study group (%) (right) from Lake Southern Konnevesi [LK-Vendace (*Coregonus albula*) and LK-Whitefish (*C. lavaretus*)], Lake Superior [LS-Cisco (*C. artedi*)], and Lake Ontario (LO-Cisco). Error bars indicate standard error.

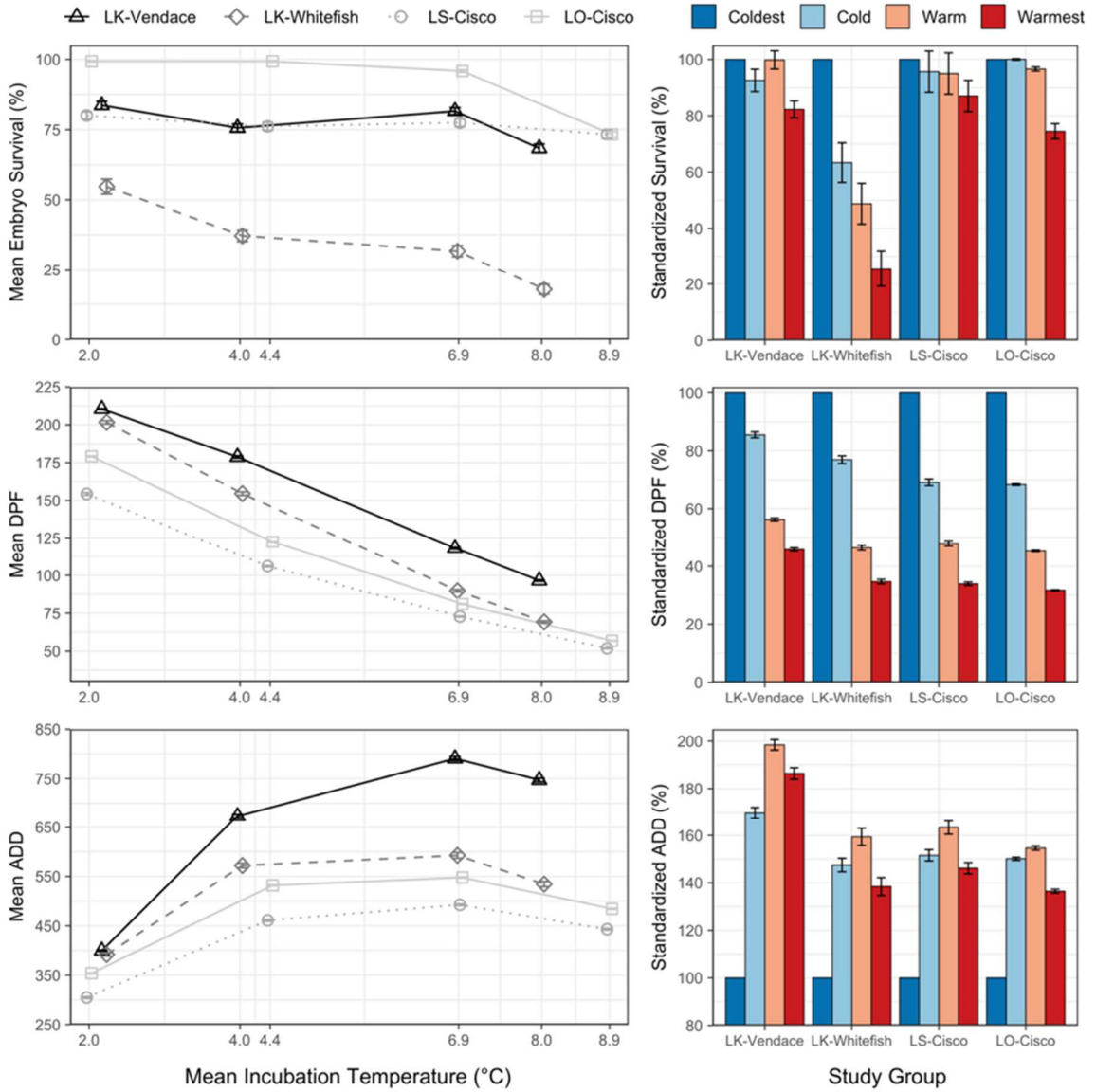


Figure 2.4: Mean percent of total phenotypic variation across incubation temperatures for embryo survival, incubation period [number of days post-fertilization (DPF) and accumulated degree days ( $^{\circ}\text{C}$ ; ADD)], length-at-hatch (mm), and yolk-sac volume ( $\text{mm}^3$ ) from Lake Southern Konnevesi vendace [LK-Vendace (*Coregonus albula*)], Lake Superior cisco [LS-Cisco (*C. artedi*)], and Lake Ontario cisco (LO-Cisco). Error bars indicate standard error.

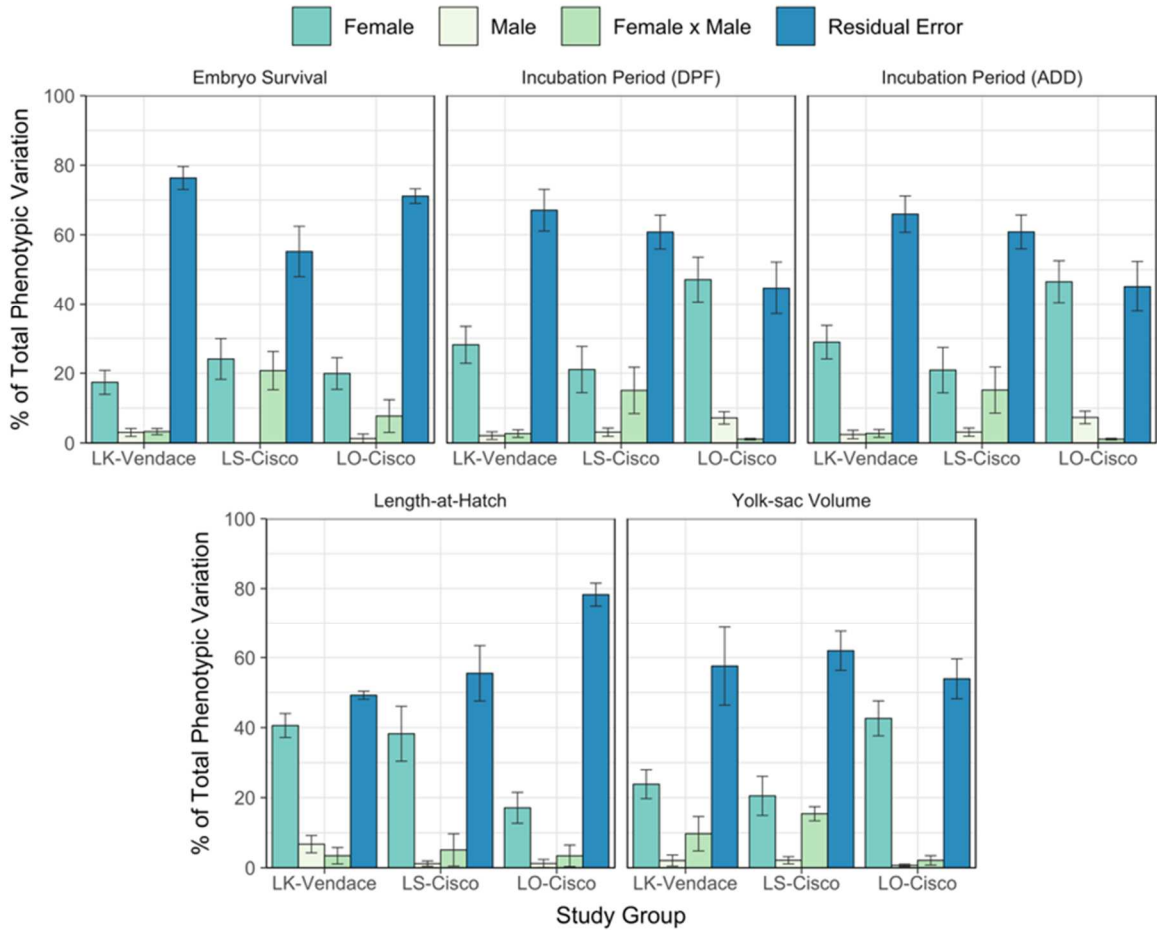
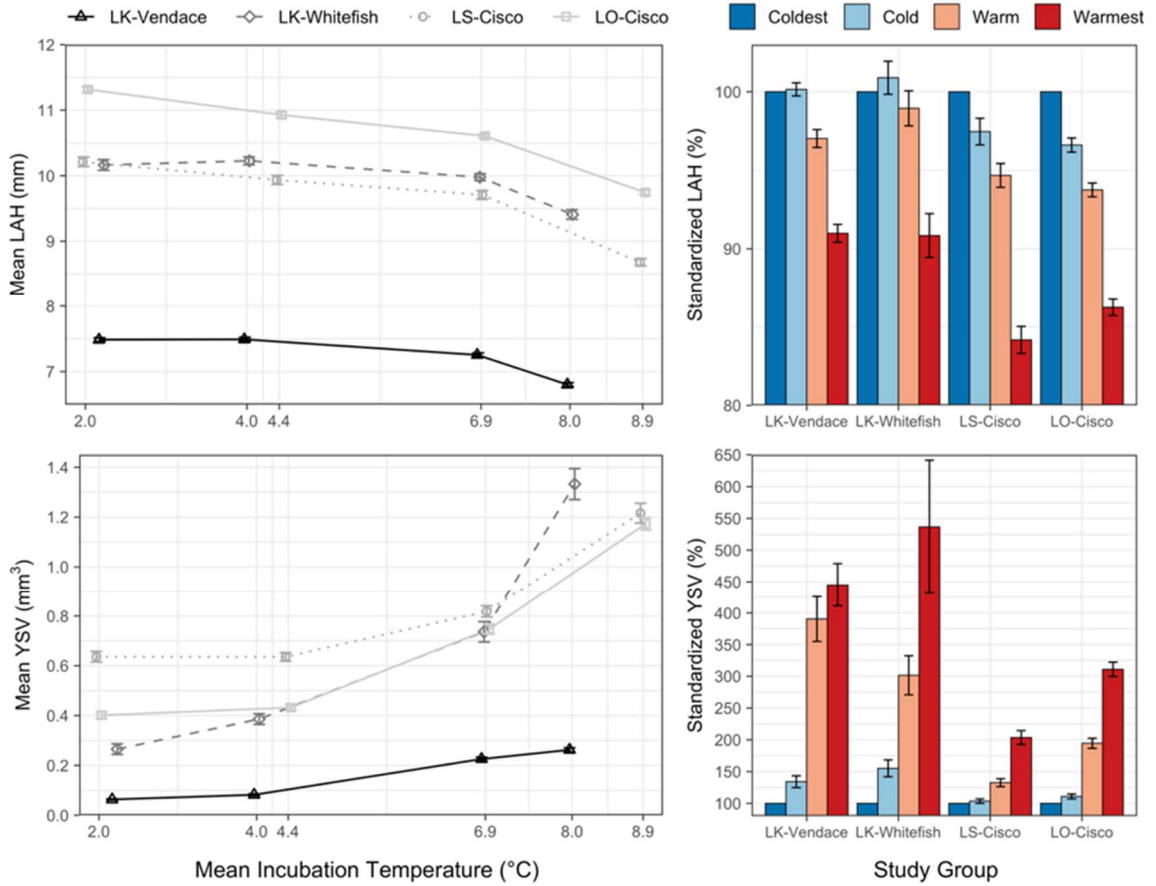


Figure 2.5: Mean length-at-hatch (mm; LAH) and yolk-sac volume (mm<sup>3</sup>; YSV) at each incubation temperature (°C; left) and standardized temperature responses within each study group (%; right) from Lake Southern Konnevesi [LK-Vendace (*Coregonus albula*) and LK-Whitefish (*C. lavaretus*)], Lake Superior [LS-Cisco (*C. artedi*)], and Lake Ontario (LO-Cisco). Error bars indicate standard error.



**CHAPTER 3: SHINING A LIGHT ON LAURENTIAN GREAT LAKES CISCO  
(*COREGONUS ARTEDI*): HOW ICE COVERAGE MAY IMPACT EMBRYONIC  
DEVELOPMENT**

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**Keywords:** *Coregonus*, cisco, climate change, embryo incubation, ice coverage, light intensity

## **Abstract**

Changes in winter conditions, such as decreased ice coverage and duration, have been observed in the Laurentian Great Lakes for more than 20 years. Such changes have been hypothesized to be linked to low *Coregonus* spp. survival to age-1 as most cisco (*Coregonus artedii*) populations are autumn spawners whose embryos incubate under ice throughout the winter. The quantity of light during winter is regulated by ice coverage, and light affects embryo survival and development in some teleosts. We experimentally evaluated how cisco embryos from lakes Superior and Ontario respond to three light treatments that represented day-light intensity under 0-10, 40-60, and 90-100% ice coverage. Embryonic response measures included two developmental factors (embryo survival and incubation period) and two morphological traits (length-at-hatch and yolk-sac volume). Embryo survival was highest at the medium light treatment and decreased at high and low treatments for both populations, suggesting cisco may be adapted to withstand some light exposure from inter-annual variability in ice coverage. Light intensity had no overall effect on length of incubation. Increasing light intensity decreased length-at-hatch in Lake Superior but had no effect in Lake Ontario. Yolk-sac volume was positively correlated with increasing light in Lake Superior and negatively correlated in Lake Ontario. Contrasting responses in embryo development between lakes suggests differences in populations' response to light is flexible. Our results provide a step towards better understanding the high variability observed in coregonine recruitment and may help predict what the future of this species may look like under current climate trends.

## **Introduction**

Freshwater whitefishes, Salmonidae Coregoninae (hereafter coregonines) play important economic (Ebener et al. 2008) and ecological (Nyberg et al. 2001; Lynch et al. 2010; Stockwell et al. 2014) roles throughout the northern hemisphere, but populations have declined over the past century (Eshenroder et al. 2016). Historical coregonine declines were attributed to overfishing, invasive species, habitat alterations, and competition (Anneville et al. 2009; Stockwell et al. 2009; Rosinski et al. 2020). More recently, coregonine populations worldwide have experienced declines due to highly variable recruitment and low survival to age-1 (Nyberg et al. 2001; Lepak et al. 2017; Parks & Rypel 2018) which have been associated with climate-induced changes in early-life stage environments (Nyberg et al. 2001). However, an underlying mechanism between changing lake environments and coregonine year-class strength has yet to be established.

Year-class strength in most fish species, including coregonines, is thought to be established prior to the end of the first season of growth (Hjort 1914; Cushing 1990; Karjalainen et al. 2015). Most coregonines are autumn spawners whose embryos incubate under ice throughout the winter (Karjalainen et al. 2000; Stockwell et al. 2009). Embryos are static, which leaves them vulnerable to predation (Stockwell et al. 2014) and unable to evade detrimental changes in winter environmental conditions (Pepin 1991). Changes in winter conditions, such as decreased ice coverage and duration, that have been observed around the northern hemisphere over the past 20+ years (Austin & Colman 2007; O'Reilly et al. 2015; Sharma et al. 2019), could alter developmental rates, embryo

survival, and time of hatching (Karjalainen et al. 2015). Potential mechanisms by which ice coverage influences coregonine embryonic development include reduced physical wave action (Walter et al. 2006; Austin & Colman 2007; Wang et al. 2010; Nguyen et al. 2017), stabilized winter and spring water temperatures (Magnuson et al. 1997; Winslow et al. 2017), and the amount of sunlight reaching the lake bottom (Bolsenga & Vanderploeg 1992; Hampton et al. 2015).

Photoperiod is the most consistent abiotic factor in nature (Ruchin 2020) and can regulate fish development phenology, behavior, and physiology (Ruchin 2007; Villamizar et al. 2011). The length of photoperiods characterize circadian rhythms and ensure that biological processes are synchronized with the environment (Marchesan et al. 2005; Gaston et al. 2013; Ruchin 2020). In seasonally ice-covered lakes, winter lake light levels are regulated by ice coverage and snow depth (Bolsenga & Vanderploeg 1992; Hampton et al. 2015). Ice can reduce light transmittance to 62% under clear ice, and to  $\leq$  10% under snow covered ice (Bolsenga & Vanderploeg 1992).

Salmonid embryos incubated under elevated light levels had higher mortality and deformity rates, slower formation of cartilaginous skeletal elements, decreased time to hatching, smaller size-at-age, and accelerated development after organogenesis (Eisler 1958; Eisler 1961; MacCrimmon & Kwain 1969; Kwain 1975; Chernyaev 2007). However, other teleosts (e.g., turbot *Scophthalmus maximus*, Atlantic halibut *Hippoglossus hippoglossus*, brown-marbled grouper *Epinephelus fuscoguttatus*) exhibit opposite responses, or no response, to manipulated light illumination during incubation (Iglesias et al. 1995; Mangor-Jensen & Waiwood 1995; Seth et al. 2014; Ruchin 2020).

To our knowledge, no previous work has examined the effects of light on coregonine embryos from North America.

We experimentally evaluated how cisco (*Coregonus artedii*) embryos responded to different photoperiod intensities, as a proxy for different ice coverages. We hypothesized that exposure to elevated light intensity (a proxy for low ice coverage) decreases embryo survival and accelerates embryogenesis, resulting in earlier hatching, larger yolk-sac volume, and shorter length-at-hatch. Our objective was to identify the extent to which light influences cisco embryo survival, incubation duration, and length and yolk-sac volume at hatching. We expected populations adapted to lower light levels (high ice coverage) would experience a greater magnitude of change as light intensity increases.

## **Methods:**

### *Ethics*

All work described here was approved for ethical animal care under University of Vermont's Institutional Animal Care and Use Committee (Protocol # PROTO202000021).

### *Study Species and Locations*

Mature cisco were collected from the Apostle Islands, Lake Superior (46.85°, -90.55°) and Chaumont Bay, Lake Ontario (44.05°, -76.20°) in December 2019. Lake Superior cisco were collected at an open lake location at depths between 15 and 50 m. Lake Ontario cisco were collected in a shallow, protected bay on rocky shoals at depths between 2 to 5 m. Egg deposition has been confirmed in Chaumont Bay (George et al.

2017; Paufve et al. 2020). No direct evidence of spawning has been observed in Lake Superior and thus we are using the presence of ripe adults at our collection location as a proxy for a spawning location. We acknowledge that spawning and the embryo incubation location could be different, but previous literature suggests that spawning in Lake Superior occurs at depths of 30-200 m (Dryer & Beil 1964; Stockwell et al. 2009; Eshenroder et al. 2016). Historical (1973-2020) ice conditions over the sampled spawning locations varied between lakes with the shallower, more protected Lake Ontario spawning site having more consistent ice coverage (i.e., relative percent of surface area within a reference grid covered by ice) between January and March than the deeper, open location in Lake Superior (Figure 3.1). Remotely-sensed vectors (i.e., SIGRID-3) produced by the North American Ice Service (<https://usicecenter.gov/Products/GreatLakesData>) were used to extract the daily percentage of ice coverage above each sampling location. The different spawning habitats provide a contrast in light levels that coregonine embryos from each population would naturally experience because maximum light availability decreases with depth (Secchi 1864; Ramus et al. 1976; Preisendorfer 1986; Fleming-Lehtinen & Laamanen 2012) and winter light availability is further restricted by ice and snow conditions (Bolsenga & Vanderploeg 1992; Hampton et al. 2015).

#### *Crossing Design and Fertilization*

Our experimental design is fully described in Stewart et al. (2021). Briefly, gametes were stripped from 12 females and 16 males from each lake and artificially fertilized to create 48 families from each lake. Reconstituted freshwater medium

(International Standards Organization 6341, 2012) was used during fertilizations and rearing to standardize the chemical properties of the water used between lakes. Embryos were transported to the University of Vermont-Burlington in coolers by overnight shipping for Lake Superior samples and driven the same day for Lake Ontario samples. A temperature logger recorded air temperature inside the transport cooler [Lake Superior: mean (SD) = 2.80°C (0.21); Lake Ontario: mean (SD) = 3.28°C (0.37)]. Total length, mass, and egg diameter were collected from the spawned adults. Fertilization success was determined by assessing 10 haphazardly selected embryos under microscopy (Oberlercher & Wanzenböck 2016). If fertilization was low (<30%), the family was removed from the experiment.

#### *Rearing Conditions*

Embryos were individually distributed into 24-well cell culture microplates and incubated in 2 ml of reconstituted freshwater (Stewart, Mäkinen, et al. 2021). A total of 36 embryos were used for each Lake Ontario and Lake Superior cisco family. Families were randomly distributed across three microplates (i.e., 12 eggs per family per microplate resulting in two families per 24-well microplate).

Microplates from each population were incubated under three light treatments that represented day-light intensity under 0-10 (low,  $0.6 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), 40-60 (medium,  $3.9 \pm 1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and 90-100 % (high,  $6.2 \pm 1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) ice coverage (Table 3.1) and followed mean weekly photoperiods with gradual sunrise and sunset transitions. Light intensities for each treatment were chosen to mimic *in situ* winter, lakebed light measurements that were previously recorded with a photometer (JFE Advantech Co., Ltd.

DEFI2-L) from Lake Superior (46.97°, -90.99°) at 10 m of water in 2016-17. No light intensity measurements were taken from Lake Ontario. Remotely-sensed vectors (i.e., SIGRID-3) produced by the North American Ice Service (<https://usicecenter.gov/Products/GreatLakesData>) were used to extract the daily percentage of ice coverage above the light sensor (Figure 3.2). Embryos were incubated at a constant target water temperature of 4.0°C in a climate-controlled chamber (Conviron® E8; Table 3.2). Forced airflow was used in the climate-controlled chamber to ensure equal air circulation around the microplates and opaque, plastic sheeting was used to separate light treatments. Microplates were covered with transparent lids to minimize evaporation and rotated (i.e., orientation and position within the incubator) weekly. Water temperature and light intensity were recorded hourly with loggers (HOBO® Water Temperature Pro v2 and JFE Advantech Co., Ltd. DEFI2-L) and daily mean values calculated (Table 3.1). During the hatch period, microplates were checked on a three-day cycle for newly hatched embryos. All hatched embryos were photographed ventrally (Nikon® D5600 and Nikon® AF-S DX 18-55mm lens) and then immediately preserved in 95% ethanol. Egg size at fertilization, total length-at-hatch, and post-hatching yolk-sac axes were measured from photographed images using Olympus® LCmicro.

#### *Developmental and Morphological Traits*

Embryo survival was estimated as the percent of embryos surviving between eye-up and post-hatch stages. Incubation period was assessed with two variables: the number of days from fertilization to hatching (days post-fertilization; DPF) and the sum of the degree-days to hatching (accumulated degree-days; ADD; °C). Total length-at-hatch

(LAH; mm) and yolk-sac volume (YSV; mm<sup>3</sup>) were measured from five individuals per family at, or as close as possible to, 50% hatching for each family. Yolk-sac volume was calculated assuming the shape of an ellipse (Blaxter & Hempel 1963):

$$YSV = \frac{\pi}{6} ab^2$$

where a = length of the yolk sac (mm) and b = height of the yolk sac (mm).

### *Statistical Analyses*

Embryo survival was analyzed as a binomial response variable, while incubation period, length-at-hatch, and yolk-sac volume at hatching were analyzed as continuous response variables. Because embryos were raised independently, the replication unit in the statistical models is the individual embryo and the design was unbalanced due to different levels of embryo mortality. All non-proportional data were visually checked for approximate normality using histograms and Q-Q plots. A cubic transformation was applied to LAH and a cubic root transformation was applied to DPF, ADD, and YSV to normalize the distributions. Embryo survival was analyzed with binomial generalized linear mixed-effects models, and the transformed variables (i.e., DPF, ADD, LAH, and YSV) were analyzed with restricted maximum likelihood linear mixed-effects models with the *lme4* package v.1.1-26 (Bates et al. 2015). Population and incubation light treatment were included as fixed effects and female, male, female x male, and fertilization block as random effects. All traits and possible interactions were examined with backward, stepwise effect-selection and the maximal model for each trait selected using the *buildmer* package v.1.7.1 (Voeten 2020). The significance for population, species, incubation temperature, interaction effects, and any random effects selected were

determined using a likelihood ratio test between the maximal model and reduced models with the model effect of interest removed.

To enable population comparisons, the response to temperature for each trait was standardized to what we assumed was the optimal light treatment - the low light treatment (Table 3.1). For each trait and family, the within-family percent change from the optimal light intensity was calculated as:

$$\frac{x_i - x_1}{x_1} \times 100;$$

where  $x_1$  = mean trait value from low light treatment and  $x_i$  = the mean trait value from the light treatment of interest. The mean among-family percent change was calculated, and standard error was calculated as the among-family variation in percent change.

All analyses were performed in R version 4.0.4 (R Core Team 2021).

## **Results:**

### *Spawning Adult and Egg Measurements*

Lake Superior spawning adults ranged from 326-503 mm (total length mean (SD) = 412.5 (40.8) mm) and 298.9-970.0 g (fresh mass mean (SD) = 589.1 (171.4) g) and were larger in total length and fresh mass than Lake Ontario adults which ranged from 321-425 mm (mean (SD) = 372.5 (25.3) mm) and 280.5-795.8 g (mean (SD) = 496.6 (126.4) g). Egg diameter was larger in Lake Ontario (mean (SD) = 2.30 (0.08) mm) than Lake Superior (mean (SD) = 2.14 (0.12) mm).

### *Developmental and Morphological Traits*

Incubation period (both DPF and ADD) and YSV had significant interaction effects between population and light treatments (maximum  $P = 0.008$ ; Table 3.3). The

interaction effects precluded any interpretation of main effects for incubation period and YSV but did suggest contrasting norms of reaction between populations. Below we describe the interaction effects for incubation period and YSV, and the population main effects and light treatment pairwise comparisons for embryo survival and LAH. All random effects (i.e., female, male, and female x male) were significant (maximum  $P = 0.009$ ) except female for embryo survival, male for embryo survival and YSV, and female x male for embryo survival and LAH (Table 3.3). All statistical model results can be found in Table 3.3.

#### Embryo Survival

Embryo survival was highest for both populations at the medium light treatment, but lowest at the low light treatment for Lake Ontario and at the high light treatment for Lake Superior (Figures 3.3 & 3.4). Light and population main effects were significant. Only Lake Ontario pairwise light treatment comparisons with the low light treatment were significant (Low - Medium  $P < 0.001$ ; Low - High  $P < 0.001$ ). All pairwise light treatment comparisons for Lake Superior were not significant (minimum  $P = 0.089$ ). Embryo survival was higher for Lake Ontario at the high (98.4%) and medium (99.6%) light treatments than for Lake Superior (85.3 and 89.3%, respectively) but there was no difference between populations at the low light treatment (0.9%; Figures 3.3 & 3.4).

#### Incubation Period

The number of days between fertilization and hatching was highest for Lake Ontario at the low light treatment (115.47 days) and for Lake Superior at the high light treatment (101.22 days; Figures 3.3 & 3.4). Lake Ontario cisco had a decrease in DPF

from the low light to the high light treatments (-0.7%), while Lake Superior had an increase from the low light to the high light treatments (1.9%; Figures 3.3 & 3.4). Incubation period (DPF) was longer for Lake Ontario than Lake Superior across all light treatments (mean (SD) difference = 13.9 (0.8) days).

The effect of light depended on population because the difference in ADD between populations was less pronounced at the high light treatment (difference = 60.8 ADD), while ADD was higher for Lake Ontario at the low and medium light treatments (497.7 and 485.9 ADD, respectively) than Lake Superior (427.5 and 420.8 ADD, respectively; Figures 3.3 & 3.4). Lake Ontario ADD had a negative response from the low to high light treatments (-2.5%), while ADD for Lake Superior did not change from the low to high light treatments (0.05%; Figures 3.3 & 3.4).

#### Length-at-Hatch

Light was not a component returned in the stepwise-selected model for length-at-hatch, but the population main effect between Lake Ontario and Lake Superior was significant ( $P < 0.001$ ; Table 3.3). Lake Ontario had a higher LAH than Lake Superior across all light treatments (Figures 3.3 & 3.4). Length-at-hatch decreased with increasing light by 3.2% in Lake Superior, but negligible differences in LAH were observed for Lake Ontario across light treatments (Figures 3.3 & 3.4).

#### Yolk-sac Volume

Yolk-sac volume had a different response to light intensity between populations (Figures 3.3 & 3.4). The effect of light depended on population because the difference in YSV between populations was less pronounced at the low light treatment (difference =

0.22 mm<sup>3</sup>), while YSV was lower for Lake Ontario at the high and medium light treatments (0.35 and 0.37 mm<sup>3</sup>, respectively) than Lake Superior (0.67 and 0.63 mm<sup>3</sup>, respectively). YSV increased from the low to high light treatments (15.3%) in Lake Superior and decreased from the low to high light treatments (-5.5%) in Lake Ontario (Figures 3.3 & 3.4).

### **Discussion:**

Developmental and morphological traits for Lake Superior and Lake Ontario cisco populations demonstrated similar and contrasting reaction norms to incubation light intensity. First, we found different responses to light intensity in embryo survival between populations. Second, increasing light intensity had minimal impact on incubation periods (DPF and ADD) for both populations. Lastly, LAH and YSV responded differently to varying light intensities between populations. Consequently, cisco from lakes Superior and Ontario are likely to have different responses to changes in ice coverage and subsequent light conditions.

Our hypothesis that embryo survival would be highest at the lowest light treatment was not supported. Embryo survival was highest for both populations at the medium light levels, suggesting that populations may be adapted to withstand some light exposure from high inter-annual variability in ice coverage. This result was contradictory to that observed in two Pacific salmonid species (chinook salmon *Oncorhynchus tshawytscha* and rainbow trout *Oncorhynchus mykiss*) for which embryo survival was highest at the lowest light exposures evaluated (0.04  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; Eisler, 1961, 1958; Kwain, 1975). Lake Ontario cisco had a sharper decrease in survival than Lake Superior

cisco at the low light treatment. The difference was surprising because average historical ice coverage over the Lake Ontario spawning location is higher than the Lake Superior spawning location, and thus low light conditions are more likely to occur for Lake Ontario cisco embryos. However, the Lake Ontario cisco spawning location is shallow (< 5 m) and could have high light intensity with little or no ice coverage. Higher variability in winter illuminance may have selected for the population of Lake Ontario cisco sampled to have greater flexibility to higher light conditions than deeper spawning cisco sampled from Lake Superior.

Our hypothesis that elevated light intensity would accelerate embryogenesis was not supported. The greatest difference in incubation periods was between populations, and was likely due to differences in embryo size, as larger embryos (i.e., Lake Ontario cisco) require more time to develop (Hodson & Blunt 1986; Kamler 2008). Previous studies of other salmonid species (European whitefish *Coregonus lavaretus*, chinook salmon, rainbow trout) found increasing light intensity decreased the length of incubation (Eisler 1958; Kwain 1975; Chernyaev 2007).

In contrast to incubation period, LAH and YSV responded to the light treatment and matched our hypotheses, but responses differed between populations. Lake Ontario cisco exhibited minimal change in LAH as light increased, but YSV decreased, suggesting that light intensity increased the metabolic demand of embryos. In comparison, Lake Superior cisco showed a trade-off between LAH and YSV. A negative relationship between LAH and YSV is common in fish temperature incubation studies (Blaxter 1991; Karjalainen et al. 2015; Stewart, Mäkinen, et al. 2021), but the

relationship is usually accompanied by a change in incubation period as basal metabolic demand consumes yolk as a function of the length of incubation. We found that light influenced incubation periods similarly among light treatments; therefore, the trade-off between LAH and YSV in Lake Superior cisco suggests decreased yolk conversion efficiency to somatic tissue occurred as light intensity increased. This suggests future decreases in ice coverage and subsequent increases in embryonic light exposure, in the absence of adaptation, may result in smaller, less-robust larvae, which may in part explain the low survival of Lake Superior cisco and other coregonines to age-1 over the past 20 years (Stockwell et al. 2009; Lepak et al. 2017). The reasons underlying differences between cisco populations from Lakes Ontario and Superior remain unknown. However, the contrasting responses in LAH and YSV between populations suggests that embryogenesis for each population has different levels of developmental plasticity to light.

Embryo development is sensitive to environmental conditions, which can greatly influence life-history trajectories, performances, and reproductive success (Colby & Brooke 1970; Luczyński 1991; Karjalainen, Jokinen, et al. 2016). We did not quantify developmental stages, except eye pigmentation, so specific life-stage developmental rates are unknown. Changes in the frequency of light (i.e., periodicity) can have adverse effects on fish embryos after yolk plug closure and first vertebrate trunk segment formation (Chernyaev 1993; Chernyaev 2007; Abdel-Rahim et al. 2019; Ruchin 2020). Fluctuating light cycles (e.g., 6:6h light:dark) and constant light (e.g., 24h light) accelerated the rate of embryonic development compared to ‘normal’ photoperiods (e.g.,

12:12h light:dark; Chernyaev, 2007, 1993; John and Hasler, 1956; Ruchin, 2020).

Photoperiod disruptions can inhibit the pineal organ and melatonin synthesis, which is critical to regulate and synchronize diurnal and seasonal biological rhythms (Roberts 1978; Delgado et al. 1987; Ekström & Meissl 1997; Falcón et al. 2010). The role photoperiod and the endocrine system plays in embryo development and phenology remains unknown for coregonines. Further studies that examine the impact of changing light intensities and photoperiods throughout incubations (e.g., decreased or no light during winter from ice coverage and increased light intensity and periodicity during spring ice-out) will help determine the fine-scale influence light and photoperiod may have on specific development stages (i.e., hatching), hormone regulation, and organ, tissue, and skeletal formation.

Sunlight intensity, albedo, and attenuation are strongly influenced by the angle of the sunlight, which is determined by season and latitude (Goldberg & Klein 1977; Forsythe et al. 1995). Latitude and sun angle are negatively correlated and this negative relationship is strongest at the winter solstice in the northern hemisphere (Goldberg & Klein 1977; Wielgolaski & Inouye 2003). Lake Ontario is at a lower latitude and thus experiences a higher sun angle than Lake Superior, which results in a more intense and longer period of daylight. Our light treatments were calculated from light sensors deployed only in Lake Superior; thus, the experimental light intensity treatments for Lake Ontario cisco may not have captured an accurate light environment representation. Under-ice light data from more lakes, depths, and habitats would add to our understanding of cisco embryo light environments and improve the authenticity of

experimental treatments. Additionally, comparing populations from high latitude lakes which experience decreased winter sunlight would provide an additional contrast for local adaptation and phenotypic plasticity across geographic regions.

Turbidity also contributes to light attenuation, and spring ice-out and river discharge can drastically increase the presence of suspended particulates and light absorption (Shao et al. 2019). Hydrological responses to climate change indicate earlier and protracted winter/spring runoff and higher runoff volume (Cutforth et al. 1999; Shen et al. 2018; Blahušiaková et al. 2020). Seasonal runoff, including snowmelt pulses, often drive high nutrient loads and primary productivity in temperate lakes (Isles et al. 2017; Rosenberg & Schroth 2017). Runoff entering ice-covered lakes is expected to suspend near the ice surface, rather than mixing into the water column (Cortés et al. 2017; Yang et al. 2020), and therefore, have implications on when nutrients are used by primary producers and the onset of spring plankton blooms (Sommer et al. 2012). If the timing of spring plankton blooms changes as a result of earlier and protracted winter/spring nutrient loads, the potential mis-match between interacting species may produce bottom-up consequences (Rogers et al. 2020). Our results showed changing light intensities did not affect cisco hatch dates; thus, the ability of cisco to match optimal spring nursery conditions may be weakened if coregonines do not respond to changing ice conditions similarly to the plankton community (Cushing 1990; Myers et al. 2015). The proximity of spawning and nursery grounds to shoreline and river outlets would likely impact the synchrony between coregonine larvae and planktonic prey.

Many fish species are iteroparous and, in some species, individuals repeatedly use the same spawning location (Marsden et al. 1995; Thorrold et al. 2001; Skjæraasen et al. 2011). The question of what constrains the choice of a spawning location cannot be separated from the question of what constrains early-life development and survival (Iles & Sinclair 1982; Sinclair & Iles 1989; Petitgas et al. 2012; Ciannelli et al. 2015). Embryo survival is largely determined by incubation habitat (e.g., water temperature, light exposure, oxygen availability, protection from predators), thus, selective pressure is focused on 'correct' and adaptive choices of spawning sites by the parents. The amount of spawning plasticity (e.g., spawning site selection, fidelity to spawning sites, spawning time) among populations could serve as an indicator for the level of evolutionary constraints for offspring (Ciannelli et al. 2015). For example, Atlantic herring (*Clupea harengus*) exhibit a wide range of reproductive strategies across diverse geographical locations, but have limited spawning site plasticity because embryo survival is dependent on substrate and vegetation (Petitgas et al. 2012). Coregonines are considered to be behaviorally and developmentally plastic and do not appear to be constrained by a spawning habitat type (Muir et al. 2013; Karjalainen et al. 2015; Pauflve 2019); however, our understanding of coregonine reproductive behavior and spawning-site selection is limited. The selection of deeper or shallower spawning locations would provide a gradient in environment conditions (e.g., light, temperature) depending on population-specific habitat requirements, and both suitable nearshore and offshore spawning habitats are historically likely to be present in each sampled lake (Goodyear 1982; Pauflve 2019).

Examining coregonine reproductive behavior and characterizing contemporary spawning habitat requirements is a logical and needed next step to build on our results.

The existence of varying trait responses between populations raises questions concerning causal mechanisms. Genomic studies can aid our understanding by determining what functional pathways could be up- or down-regulated due to light energy. Any potential changes in metabolic or catabolic genes from light will enhance trait analyses and allow further partitioning of the effects of light from other energy demanding environmental variables (e.g., temperature).

**Conclusion:**

Given the extensive degree of developmental plasticity in coregonines, propagation has been proposed as a practical way to reintroduce native species from lakes with extirpated or reduced population levels (Zimmerman & Krueger 2009; Bronte et al. 2017). A key uncertainty to maximizing restoration efforts is whether managers should mimic natural environmental conditions to increase survival during propagation (Bronte et al. 2017). Our study highlights the potential role of winter light conditions, the influence of light intensity on cisco embryo development, and the impact changing ice regimes may have on cisco survival and recruitment in the wild. We did not identify a consistent directional reaction between and within the two sampled cisco populations to increasing light, and light is likely to have a differential effect on a number of physiological and biochemical processes. Large-scale, cross-lake propagation and reintroduction efforts are likely to be complicated by the capacity to match cisco phenotypes and optimal incubation conditions. Our results provide a step towards better

understanding the recent high variability observed in coregonine recruitment and may help predict what the future of this species may look like under current climate trends.

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Table 3.1: Mean daily  $\pm$  SD light intensity ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) for three ice coverage (i.e., relative percent of surface area within a reference grid covered by ice) classes measured from a light sensor set at 10 m depth off Sand Island, Lake Superior and corresponding laboratory experimental light conditions used for both Lake Superior and Lake Ontario. Ice coverage was extracted from remotely-sensed vectors (i.e., SIGRID-3) at the coordinates of the field light sensor (North American Ice Service; <https://usicecenter.gov/Products/GreatLakesData>).

Location	Ice Coverage (Light Treatment)		
	> 90% (Low)	40-60% (Medium)	< 10% (High)
Field (Lake Superior)	2.0 $\pm$ 1.1	3.4 $\pm$ 2.5	5.5 $\pm$ 5.9
Laboratory	0.6 $\pm$ 0.1	3.9 $\pm$ 1.9	6.2 $\pm$ 1.0

Table 3.2: Mean daily  $\pm$  SD water temperatures ( $^{\circ}\text{C}$ ) during embryo incubations from each light treatment for Lakes Superior and Ontario. Light treatment levels correspond to 0-10 (low,  $0.6 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), 40-60 (medium,  $3.9 \pm 1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and 90-100 % (high,  $6.2 \pm 1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) ice coverage.

Lake	Light Treatment		
	High	Medium	Low
Superior	$4.3 \pm 0.2$	$4.3 \pm 0.3$	$4.3 \pm 0.3$
Ontario	$4.2 \pm 0.3$	$4.3 \pm 0.3$	$4.4 \pm 0.4$

Table 3.3: Likelihood ratio test output for each model selected for embryo survival (%), incubation period [number of days post-fertilization (DPF) and accumulated degree days ( $^{\circ}\text{C}$ ; ADD)], length-at-hatch (mm), and yolk-sac volume ( $\text{mm}^3$ ) from Lakes Superior and Ontario cisco (*Coregonus artedii*). pop indicates population. The full model that was selected is bolded for each trait.

Trait	Model	Effect Tested	df	$\chi^2$	p-value
Embryo Survival	<b>light + pop</b>				
	pop	light	2	181.92	< 0.001
	light	pop	1	95.00	< 0.001
Incubation Period (DPF)	<b>light + pop + light:pop + family + female + male</b>				
	pop + family + female + male	light	2	10.80	0.005
	light + family + female + male	pop	1	3,023.89	< 0.001
	light + pop + family + female + male	light:pop	2	9.66	0.008
	light + pop + light:pop + female + male	family	1	79.91	< 0.001
	light + pop + light:pop + family + male	female	1	25.29	< 0.001
	light + pop + light:pop + family + female	male	1	10.80	0.001
Incubation Period (ADD)	<b>light + pop + light:pop + family + female + male</b>				
	pop + family + female + male	light	2	51.72	< 0.001
	light + family + female + male	pop	1	3,092.41	< 0.001
	light + pop + family + female + male	light:pop	2	13.23	0.001
	light + pop + light:pop + female + male	family	1	79.99	< 0.001
	light + pop + light:pop + family + male	female	1	25.25	< 0.001
	light + pop + light:pop + family + female	male	1	10.75	< 0.001
Length-at-Hatch	<b>pop + female + male</b>				
	female + male	pop	1	373.34	< 0.001
	pop + male	female	1	100.97	< 0.001
	pop + female	male	1	11.37	< 0.001
Yolk-sac Volume	<b>light + pop + light:pop + family + female</b>				
	pop + family + female	light	2	1.96	0.376
	light + family + female	pop	1	712.18	< 0.001
	light + pop + family + female	light:pop	2	19.04	< 0.001
	light + pop + light:pop + female	family	1	6.52	< 0.001
	light + pop + light:pop + family	female	1	38.94	< 0.001

Figure 3.1: Histogram of annual mean ice coverage (i.e., relative percent of surface area within a reference grid covered by ice) between 1-Jan and 15-Mar from 1973-2020 for the sampling location in Lake Superior (top) and Lake Ontario (bottom). Ice coverage was extracted from remotely-sensed vectors (i.e., SIGRID-3) at the coordinates of each sampling location (North American Ice Service; <https://usicecenter.gov/Products/GreatLakesData>).

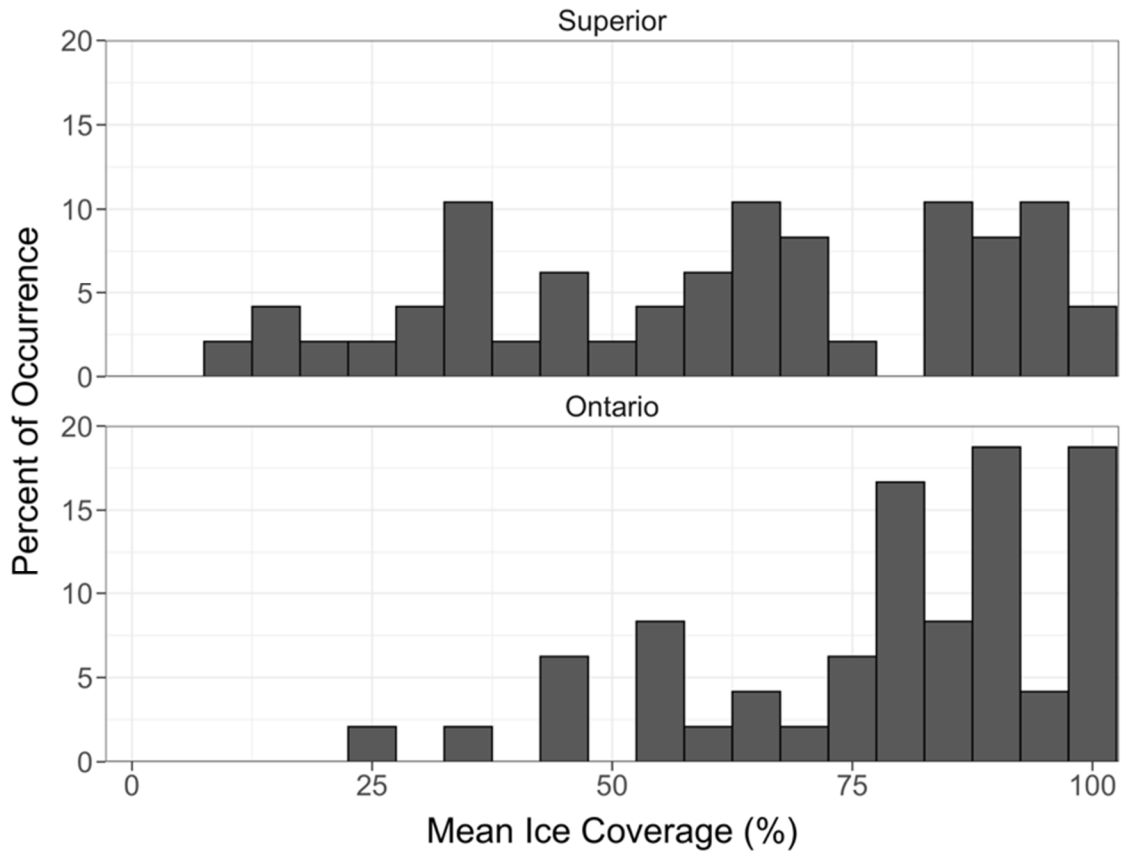


Figure 3.2: Daily ice coverage (i.e., relative percent of surface area within a reference grid covered by ice; blue line) and light intensity ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; gray line) based on a light sensor set at 10 m depth off Sand Island, Lake Superior. Ice coverage was extracted from remotely-sensed vectors (i.e., SIGRID-3) at the coordinates of the field light sensor (North American Ice Service; <https://usicecenter.gov/Products/GreatLakesData>).

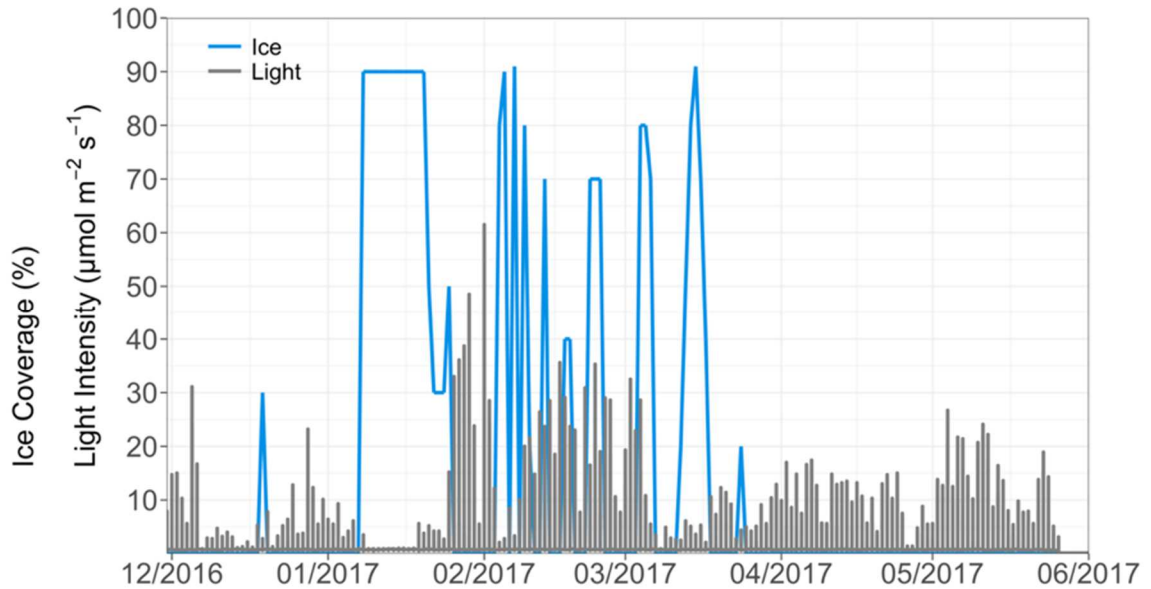


Figure 3.3: Mean embryo survival (%), length-at-hatch (mm; LAH), yolk-sac volume (mm<sup>3</sup>; YSV), and incubation period [number of days post-fertilization (DPF) and accumulated degree days (°C; ADD)] at each incubation light treatment from Lake Superior and Lake Ontario cisco (*Coregonus artedii*). Light treatment levels correspond to 0-10 (low,  $0.6 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), 40-60 (medium,  $3.9 \pm 1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and 90-100 % (high,  $6.2 \pm 1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) ice coverage. Error bars indicate standard error.

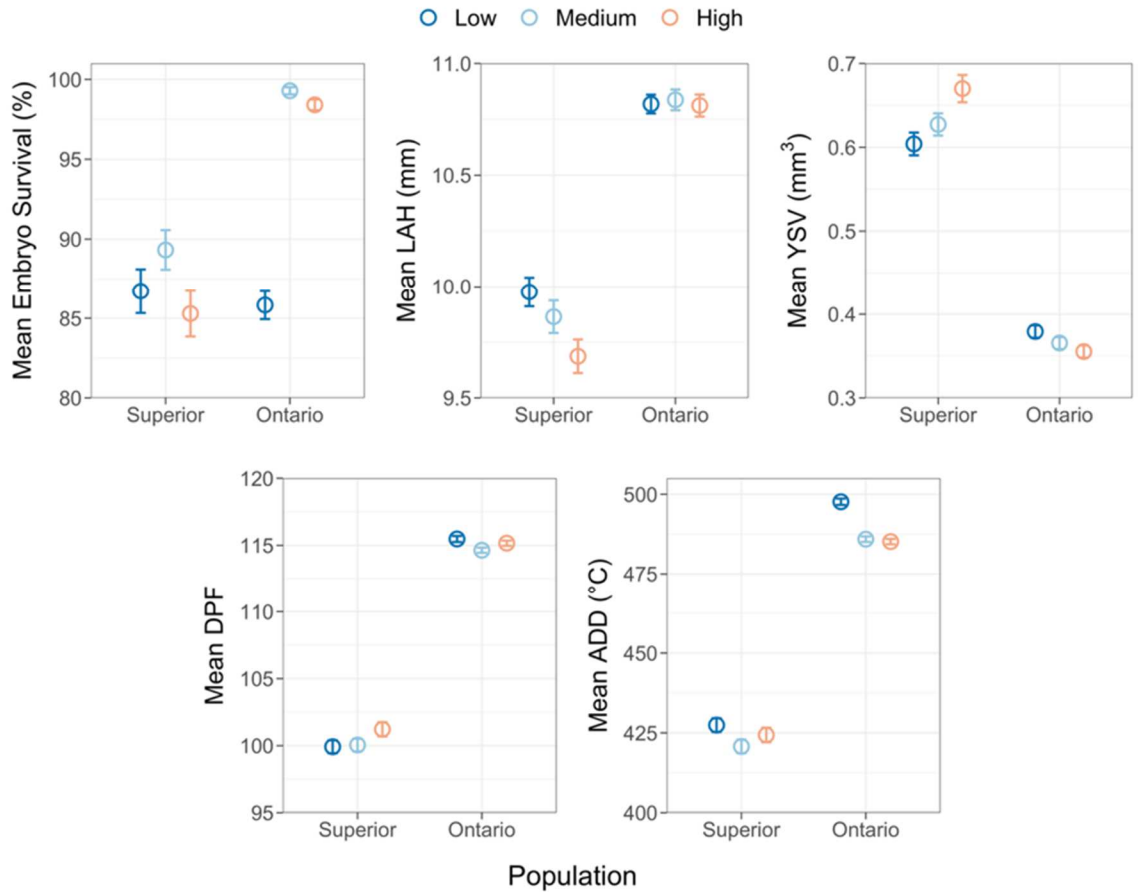
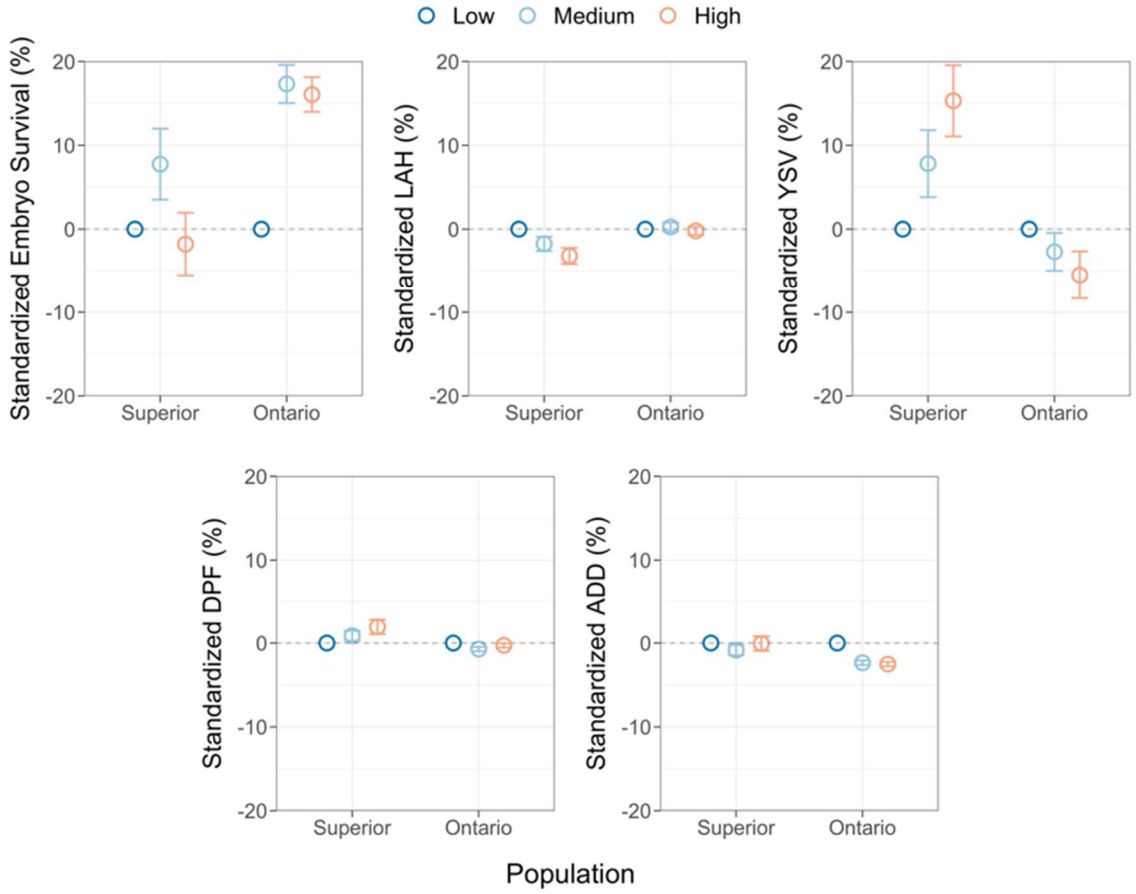


Figure 3.4: Mean among-family standardized responses (%) to assumed optimal light conditions (i.e., low) within each sampled population from Lake Superior and Lake Ontario cisco (*Coregonus artedii*) for embryo survival, length-at-hatch (LAH), yolk-sac volume (YSV), and incubation period [number of days post-fertilization (DPF) and accumulated degree days (ADD)] at each incubation light treatment. Light treatment levels correspond to 0-10 (low,  $0.6 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), 40-60 (medium,  $3.9 \pm 1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and 90-100 % (high,  $6.2 \pm 1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) ice coverage. Error bars indicate among-family standard error.



**CHAPTER 4: EFFECTS OF WARMING WINTER EMBRYO INCUBATION  
TEMPERATURES ON LARVAL CISCO (*COREGONUS ARTEDI*) SURVIVAL,  
GROWTH, AND CRITICAL THERMAL MAXIMUM**

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## **Abstract**

Freshwater whitefishes, Salmonidae Coregoninae, are cold stenothermic fishes of ecological and socio-economic importance in northern hemisphere lakes that are warming in response to climate change. To address the effect of warming waters on coregonine reproduction we experimentally evaluated different embryo incubation temperatures on post-hatching survival, growth, and critical thermal maximum of larval cisco (*Coregonus artedi*) sampled from lakes Superior and Ontario. Embryos were incubated at water temperatures of 2.0, 4.4, 6.9, and 8.9°C to simulate present and increased winter temperatures, and hatched larvae were reared in a common environment. For both populations, larval survival and critical thermal maximum were negatively related to incubation temperature, and larval growth was positively related to incubation temperature. The magnitude of change across incubation temperatures was greater in the population sampled from Lake Superior than Lake Ontario for all traits examined. The more rapid decrease in survival and critical thermal maximum across incubation temperatures for larval cisco in Lake Superior, compared to those from Lake Ontario, suggests that Lake Superior larvae may possess a more limited ability to acclimate to and cope with increasing winter water temperatures. However, the rapid increase in growth rates across incubation temperatures in Lake Superior larvae suggests they could recover better from hatching at a small length induced by warm winters, as compared to Lake Ontario larvae. Our results suggest propagation and restoration programs may want to consider integrating natural habitat preferences and maximizing phenotypic variability to ensure offspring are set up for success upon stocking.

## **Introduction**

Water temperatures are rising around the globe (Austin & Colman 2008; O'Reilly et al. 2015; Maberly et al. 2020; Woolway et al. 2020) and poses a threat to ectotherms, such as fish, that have limited thermal tolerance ranges (Comte & Olden 2017; Dahlke et al. 2020; Little et al. 2020). Thermal tolerances vary with ontogenetic development (Dahlke et al. 2020; Sunday 2020) and affect reproduction, metabolic rates, growth, and overall survival (Brett 1979; Gillooly et al. 2002; Brown et al. 2004; Ohlberger et al. 2007; Busch et al. 2012; Little et al. 2020). Vulnerability of fishes to climatic warming is highest for cold stenothermic species that lack the ability to migrate to suitable temperatures. Specific vulnerability of local populations will likely depend on future climate regime shifts and the temperature requirements of spawners and embryos (Dahlke et al. 2020; Sunday 2020). In the short-term, lacustrine spawners may cope with warming waters by shifting spawning timing or using deeper and colder spawning habitat, or potentially in the long-term through thermal adaptation across generations. Adaptation, however, may be too slow to keep pace with changing thermal conditions (Bruge et al. 2016). For autumn to winter spawners, spawning later in the season after waters have cooled sufficiently may still impact embryo development due to warmer winter temperatures and earlier spring warming.

Freshwater whitefishes, Salmonidae Coregoninae (hereafter coregonines), are cold, stenothermic fishes of ecological and socio-economic importance throughout the northern hemisphere (Stockwell et al. 2009; Elliott & Bell 2011; Jeppesen et al. 2012; Isaak 2014; Jonsson & Jonsson 2014; Karjalainen et al. 2015). In the Laurentian Great

Lakes, cisco (*Coregonus artedi*) was historically the most abundant ciscoe (*sensu* Eshenroder et al., 2016) species, a primary prey fish of lake trout (*Salvelinus namaycush*), and a commercial fishing target since the early 1800s (Bogue 2001; Chiarappa 2005). Most cisco spawning stocks collapsed by the mid-1900s (Koelz 1929; Baldwin et al. 2009). Lake Superior stocks partially recovered by the early-1990s (Stockwell et al. 2009), but contemporary abundance is considered to be below historical levels (Rook et al. 2021). Present Lake Superior cisco population abundance is hypothesized to be limited by reduced and inconsistent survival of fish to age-1 due to climatic warming over the past two decades (Van Cleave et al. 2014) and lower overall ecosystem productivity due to reduced phosphorus inputs as compared to 1900-1970 (Rook et al. 2021). Variable and weak year-class strength of coregonines has been observed worldwide over the past several decades and has been associated with annual variations in lake ice formation and winter-spring thermal conditions (Nyberg et al. 2001; Marjomäki et al. 2004; Anneville et al. 2015; Karjalainen et al. 2015).

Most coregonines spawn nearshore in late-autumn, embryos incubate under ice, and hatch in spring near ice-out, when rising spring water temperatures trigger hatching (Stockwell et al. 2009; Karjalainen et al. 2015; Karjalainen et al. 2019; Karjalainen et al. 2021). Increases in air temperature and water temperatures of seasonally ice-covered lakes are projected to be greatest during the winter and spring, respectively, in response to climate change (Schindler et al. 1990; Christensen et al. 2007; Winslow et al. 2017; Ozersky et al. 2021).

The larval period of fishes is critical for year-class success (Hjort 1914; Cushing 1990), but the physiological effects of thermal stress from non-optimal embryo incubation temperatures on post-hatching survival are unclear. Additional physiological pressures as a result of warming winter temperatures could be detrimental. The match-mismatch hypothesis postulates that larval survival is dependent on a temporal and spatial match between larval feeding capabilities, such as swimming ability and prey acquisition, and prey availability (Cushing 1990). Warmer incubation temperatures lead to earlier hatch dates and altered morphological developments, such as smaller lengths and larger yolk sacs, that reduce larval feeding efficiency (Dabrowski et al., 1988), compared to colder incubated embryos (Karjalainen et al. 2015; Stewart, Mäkinen, et al. 2021). The selective pressures from elevated temperatures on embryonic and larval coregonine development and survival may lead to adaptation, but the thermal trigger for the response and the mechanism of the response are unknown. Consequently, quantifying the potential response and adaptive capacity of cisco to warming winter and spring water temperatures is needed.

We experimentally evaluated how cisco embryo incubation temperatures influenced the survival and performance of hatching larvae within and between two Great Lakes cisco populations. We hypothesized that warmer, sub-optimal cisco embryo incubation temperatures decrease larval survival, growth, and critical thermal limits compared to embryo incubation temperatures that mimic cold, pre-climate change conditions. If our hypothesis is supported, we would expect a negative relationship

between embryo incubation temperature and the larval traits examined for wild cisco populations when reared artificially.

## **Methods**

### *Ethics*

All work described here was approved for ethical animal care under University of Vermont's Institutional Animal Care and Use Committee (Protocol # PROTO202000021).

### *Crossing Design and Fertilization*

Cisco were collected from the Apostle Islands, Lake Superior (46.85°, -90.55°) and Chaumont Bay, Lake Ontario (44.05°, -76.20°) in December 2019. Eggs and milt were stripped from 12 females and 16 males from each population and artificially fertilized under a blocked, nested full-sib, half-sib fertilization design to create a maximum of 48 families. A single fertilization block consisted of four males each paired to three unrelated females, where all offspring of a given female were full siblings (Stewart, Mäkinen, et al. 2021).

For clarity, our operational use of a population represents a single species sampled from a single location within a single lake (e.g., cisco from the Apostle Islands region in Lake Superior). Our sampling efforts represent a single location within large lakes and does not likely capture the possible genetic variation within a species or population.

### *Rearing Conditions*

Full embryo incubation methods are described in Stewart et al. (2021). Embryos were incubated in 24-well cell culture microplates placed in climate-controlled chambers (Memmert<sup>®</sup> IPP260Plus) at mean (SD) constant temperatures of 2.0 (0.5), 4.4 (0.2), 6.9 (0.2), and 8.9 (0.3)°C. These temperatures were selected to mimic present and potentially warmer winter temperatures (Titze & Austin 2014) at typical cisco spawning depths (<100 m, Goodyear, 1982). Reconstituted freshwater medium was used during fertilizations and incubations (International Organization For Standardization 6341, 2012) to standardize the chemical properties of the water among all treatments and between populations. After hatching, larvae were photographed alive and ventrally (Nikon<sup>®</sup> D5600 and Nikon<sup>®</sup> AF-S DX 18-55mm lens). Total length was measured from images using Olympus<sup>®</sup> LCmicro.

Newly-hatched larvae were transferred to rearing tanks segregated by population and incubation temperature. Larvae from Lake Superior were reared in four (4 incubation treatments x 1 replicate) 150-liter oval tanks. Larvae from Lake Ontario were reared in eight (4 incubation treatments x 2 replicates) 150-liter oval tanks. Lake Ontario larvae were divided equally by families (i.e., up to 24 of 48 total larvae per family per replicate tank) into replicate tanks per incubation temperature treatment. Lake Superior larvae were unreplicated as a result of low fertilization success and embryo survival - insufficient numbers were available for multiple rearing tanks. All rearing tanks were supplied with chilled, recirculating water maintained at 6.5°C [mean (SD) = 6.36 (1.17)]. Water temperatures ( $\pm 0.2^\circ\text{C}$ ) were recorded hourly. Larvae in all rearing tanks were exposed to the same photoperiod cycle (i.e., 12-hr light, 12-hr dark) with gradual sunrise

and sunset transitions. Full spectrum (i.e., 380-780 nm), white LED lights (AquaShift<sup>®</sup> MLA-WH) were used to simulate daylight. Dead larvae were removed and counted each day. Larvae were fed Artemia immediately upon hatch and transitioned to Otohime A1 (75-150  $\mu$ m) dry feed one-week post-hatch. Food was provided once daily by hand and ad libitum.

### *Thermal Challenge*

After 60 days post-hatch, larvae from each population, incubation treatment, and replicate rearing tank were thermally challenged. Because larvae within and among rearing tanks did not hatch on the same day, 60-days post-hatch was calculated from the date of 50% hatching for each rearing tank. Larvae were transferred to 5.4-liter clear, rectangular tanks, with two replicate tanks per rearing tank and approximately 50 larvae, or as many available, were used in each replicate tank. Water temperature was 10°C and larvae were allowed to acclimate to this temperature for 12 hours prior to the thermal challenge. The water in the thermal challenge system was recirculated among all replicate tanks and aerated. During the thermal challenge, water temperatures were raised from 10.0°C at a constant rate of 0.5°C per 30 minutes until all larvae were deceased. Larvae were considered terminated when loss of equilibrium was achieved and were motionless for at least 5 seconds. Once endpoint criteria were met, larvae were euthanized (AQUI-S<sup>®</sup> 20-E), photographed, and preserved in 95% ethanol. The elapsed time from the start of acclimation to termination and temperature at termination of each individual larvae was recorded and total length was measured from the images.

All larvae from the 8.9°C treatment died during the acclimation period from an unknown cause, thus, only thermal challenge data from 2.0, 4.4, and 6.9°C are presented.

### *Statistical Analyses*

All statistical analyses were performed in R version 4.0.5 (R Core Team 2021).

Larval survival was estimated for each rearing tank, across all families, as the percent of larvae surviving between hatching and 60 days after the date of 50% hatching. Our estimates of larval survival from Lake Superior are unreplicated. However, useful information can still be gleaned without strict statistical testing (e.g., Davies and Gray, 2015). Observations of single estimates of larval survival across incubation temperatures could foster further hypotheses and lead to more focused studies.

Similar to larval survival estimates, larval growth rate estimates for Lake Superior were unreplicated. To this end, we qualitatively compared absolute growth rates between populations and across incubation temperatures by generating bootstrapped confidence intervals for the observed absolute growth rate estimates. For each population, incubation temperature treatment, and replicate rearing tank, a bootstrapped mean length-at-hatch was calculated from random sampling with replacement from the observed lengths-at-hatch, and a bootstrapped mean final length was calculated from random sampling with replacement from the observed final lengths. The difference between the bootstrapped mean final length and bootstrapped mean length-at-hatch was calculated and divided by the duration of the larval experiment (i.e., absolute growth rate). The bootstrap procedure was repeated 10,000 times. The bootstrapped absolute growth rate distributions were used to calculate the 2.5 and 97.5 percentile values (i.e., 95% confidence interval) as a

measure of variation around the observed absolute growth rate, and to qualitatively assess the likelihood of differences in growth among populations and incubation temperature treatments, in absence of replication. For Lake Ontario, the 95% confidence intervals were calculated as the mean 2.5 and 97.5% percentiles across replicate tanks. Comparisons were made by examining the overlap of the observed mean absolute growth rate to the bootstrapped 95% confidence intervals of all pairwise comparisons.

The critical thermal maxima (CTMax) of larval cisco from each population and incubation temperature treatment was expressed as the arithmetic mean of the temperature at which endpoint criteria were reached (Mora & Ospina 2001). Although we have estimates for each individual larva within replicate thermal challenge tanks, the larvae from Lake Superior were reared in a single rearing tank and thus the estimates are not independent and cannot be treated as true replicates. Therefore, a similar bootstrap approach as described for larval growth was used to qualitatively compare CTMax among populations and incubation temperature treatments. For each population, incubation temperature treatment, and replicate rearing tank, we generated a bootstrap sample by randomly selecting, with replacement, a termination temperature  $n$  times, where  $n$  equals the number of observations in the experiment. The CTMax was calculated for each bootstrapped sample and the distribution of bootstrapped CTMax was used to calculate the 95% confidence interval as a measure of variation around the observed CTMax. The bootstrap procedure was repeated 10,000 times. For Lake Ontario, the 95% confidence intervals were calculated as the mean 2.5 and 97.5% percentiles across

replicate tanks. Comparisons were made by examining the overlap of the observed mean CTMax to the bootstrapped 95% confidence intervals of all pairwise comparisons.

## **Results**

### *Larval Survival*

A total of 9,605 larvae hatched and were reared from lakes Superior (2,332 larvae) and Ontario (7,273 larvae) across all incubation temperatures. Larval survival was highest at the 2.0°C incubation temperature and decreased with warming incubation temperatures for both populations (Figure 4.1). Survival rates were 38.7% at 2.0°C, 17.7% at 4.4°C, 1.1% at 6.9°C, and 5.4% at 8.9°C for Lake Superior larvae and 43.3% at 2.0°C, 35.3% at 4.4°C, 12.4% at 6.9°C, and 2.6% at 8.9°C for Lake Ontario larvae. Larval survival was higher for Lake Ontario larvae than Lake Superior larvae across all incubation temperature treatments, except 8.9°C. Lake Ontario larvae had similar survival rates (< 9% difference) at the 2.0 and 4.4°C incubation temperatures, whereas Lake Superior larval survival decreased 21% from the 2.0° to 4.4°C incubation temperatures (Figure 4.1).

### *Larval Growth*

Larval cisco absolute growth rates increased with warming incubation temperatures in both populations (Figure 4.2). Larvae from Lake Superior had lower absolute growth rates at 2.0 and 4.4°C (0.049 and 0.044 mm day<sup>-1</sup>, respectively) compared to Lake Ontario (0.056 and 0.061 mm day<sup>-1</sup>, respectively). Absolute growth rates were highest at 6.9°C for Lake Superior (0.057 mm day<sup>-1</sup>) and 8.9°C for Lake Ontario (0.078 mm day<sup>-1</sup>), and both populations had similar absolute growth rates

between 6.9 and 8.9°C (mean difference <0.001 and 0.012 mm day<sup>-1</sup>, respectively; Figure 4.2).

### *Thermal Challenge*

Critical thermal limit in larval cisco decreased with warming incubation temperatures in Lake Superior and Lake Ontario (Figure 4.3). Larvae from Lake Superior incubated at 2.0°C had the highest CTMax (25.81°C). However, CTMax in Lake Superior decreased by 0.83 and 0.77°C between the 2.0 to 4.4°C and the 4.4 and 6.9°C incubation temperature treatments, respectively. CTMax was similar for Lake Ontario larvae incubated at 2.0 and 4.4°C (24.99 and 24.96°C, respectively) and decreased at 6.9°C (24.67°C).

### **Discussion**

Survival, growth rates, and critical thermal limits of cisco larvae from lakes Superior and Ontario were influenced by embryo incubation temperatures that were warmer than current natural winter water temperatures in these lakes. First, we found a negative relationship between larval survival and embryo incubation temperature. Second, warmer embryo incubation temperatures increased larval growth rates. Third, critical thermal limits decreased with warming incubation temperatures. Lastly, the magnitude of change across incubation temperature treatments was greater in cisco from the historically colder Lake Superior than Lake Ontario for all traits examined. These results suggest increased risk to Laurentian Great Lakes cisco populations in response to projected climatic warming.

Our hypothesis that larval survival is highest at the coldest incubation temperature, which mimicked the natural lake environment, was supported. Between the two lakes, Lake Superior cisco had a sharper decline in larval survival from 2.0 to 4.4°C compared to Lake Ontario cisco. Though both populations are cold adapted, the result suggests Lake Superior cisco were more cold-water adapted than those from Lake Ontario. Lake Superior is colder than Lake Ontario (Millar 1952; Mason et al. 2016) and spawning cisco from Lake Superior were collected at an open lake location, whereas spawning cisco from Lake Ontario cisco were collected in a shallow, protected bay. Water temperatures in shallower protected habitats increase more rapidly after ice-out and have higher maximum spring and summer temperatures (*i.e.*, Lake Ontario sampling location; Minns et al., 2011) compared to deeper, open-water locations (*i.e.*, Lake Superior sampling location; Titze and Austin, 2014) because the heat capacity of water is positively related to depth and water is mixed less in protected bays (Assel et al. 2003; Verburg & Antenucci 2010; Gan & Liu 2020). Interactions among winter and spring temperatures, hatching dates, zooplankton availability and larval size-dependent predation mortality influence year-class strength of vendace (*C. albula*) and European whitefish (*C. lavaretus*) in Europe (Miller et al. 1988; Marjomäki et al. 2004; Anneville et al. 2009; Mehner et al. 2011). Spring warming rates in particular appear to play a critical role in prey availability and larval growth and survival of autumn-spawning coregonines (Myers et al. 2014; Karjalainen et al. 2015).

The transition from endogenous to exogenous feeding is critical to larval fish survival (Hjort 1914; Cushing 1990). Higher winter temperatures induce earlier

coregonine embryo hatching and cause larvae to have smaller lengths-at-hatch and larger yolk-sac volumes (Karjalainen et al. 2015; Stewart, Mäkinen, et al. 2021). Larvae hatching with larger yolk sacs may have more time to transition to exogenous feeding (Hjort 1914; Miller et al. 1988; Lucke et al. 2020), but at a cost to swimming efficiency and predator avoidance (Dabrowski et al., 1988; Myers et al., 2014). In wild populations, earlier hatching may also increase the mismatch between the onset of spring plankton blooms and larval prey, increasing the risk for starvation and higher larval mortality (Cushing 1990; Myers et al. 2014). Interactions among winter and spring temperatures, hatching dates, zooplankton availability and larval size-dependent predation mortality influence year-class strength of vendace (*C. albula*) and European whitefish (*C. lavaretus*) in Europe (Miller et al. 1988; Marjomäki et al. 2004; Anneville et al. 2009; Mehner et al. 2011). Spring warming rates in particular appear to play a critical role in prey availability and larval growth and survival of autumn-spawning coregonines (Myers et al. 2014; Karjalainen et al. 2015). Our experiment provided cisco larvae a predator-free environment with *ad libitum* food immediately after hatching, yet we still observed sharp declines in larval survival for those incubated at increased temperatures. We suggest an additional or alternative hypothesis for a survival bottleneck under climate change scenarios is that larval cisco survival may not be as limited by prey availability but instead by reduced physiological condition caused by warmer embryo incubations.

Rapid larval growth is associated with high survival (Ware 1975; Blaxter 1986; Miller et al. 1988; Houde 1989a; Myers et al. 2014). In our experiment, larval cisco exhibited low survival despite higher absolute growth rates when incubated at warmer

temperatures. These results did not support our hypothesis that warmer, sub-optimal cisco incubation temperatures decrease larval growth rates. Coregonine embryos incubated at high temperatures (i.e.,  $> 6^{\circ}\text{C}$ ) often hatch prematurely and are underdeveloped (Price 1940; Colby & Brooke 1970). Warmer incubations may require free-floating embryos to rapidly convert yolk for development. In this sense, higher absolute growth rates gained from warming incubation temperatures may not be optimal for survival. Larval cisco from Lake Superior use a mixed-feeding strategy with endogenous energy reserves (i.e., yolk) and exogenous feeding overlapping at lengths between 10.0-12.0 mm (Lucke et al. 2020). Embryos incubated at colder temperatures (i.e.,  $2.0$  and  $4.4^{\circ}\text{C}$ ) from the sampled populations of lakes Superior and Ontario cisco had mean lengths-at-hatch from 9.9-11.3 mm, whereas mean lengths-at-hatch ranged from 8.7-9.7 mm at the warmest incubation temperature ( $8.9^{\circ}\text{C}$ ; Stewart, Mäkinen, et al. 2021; Stewart, Vinson, et al. 2021a). A combination of field and experimental data suggests that cold, long incubations with prolonged development results in larger length-at-hatch with less endogenous energy reserves, the ability to immediately use a mixed endogenous and exogenous feeding strategy, and lower growth rates could be the best scenario to maximize larval survival (Lucke et al. 2020; Stewart, Mäkinen, et al. 2021). However, this ‘goldilocks scenario’ may only work if all biotic and abiotic conditions (e.g., water temperature, appropriately sized prey, etc.) match cisco phenotypes. This hypothesis remains to be tested, as our experiments provided a stable and optimal temperature and feeding environment, conditions that cannot be assumed to occur in the wild.

The ability of larval cisco to use favorable nursery habitat near the lake surface is directly related to their ability to tolerate spring-summer surface water temperatures. The increase in CTMax with decreased incubation temperature supported our hypothesis that cold, pre-climate change conditions would maximize thermal performance. The different magnitudes of change between cisco from lakes Superior and Ontario could be explained from evolutionary adaptations to local conditions. Fish populations from high-latitude, low-temperature locales often compensate for slower metabolism and lower growth rates by having more efficient physiological performance than low-latitude populations (*i.e.*, countergradient variation; (Conover & Present 1990; Jonassen et al. 2000; Reist et al. 2006). Lake Superior experiences colder and less seasonal variation in water temperature than Lake Ontario (Zhang et al. 2018; Calamita et al. 2021), and larval cisco from Lake Superior may have more efficient physiological adaptations (*e.g.*, cardiac and respiratory performance) which could explain the high thermal tolerance at cold incubation temperatures and sensitivity to increased temperatures. Our results suggest research on mechanisms driving the observed differences in CTMax between populations (*e.g.*, cardiac failure, oxidative damage to tissue, body mass, stress biomarkers, protein denaturation, etc.) may prove insightful.

Our results have implications for current and proposed hatchery-based restoration efforts of coregonines in the Laurentian Great Lakes (Bronte et al. 2017). We found that cisco offspring from two of the Great Lakes raised at warm incubation temperatures (*i.e.*, > 4.5°C) had lower overall performance than individuals incubated at cold temperatures

(*i.e.*,  $< 4.5^{\circ}\text{C}$ ). Many coregonine hatchery facilities around the Great Lakes do not or cannot incubate embryos under natural lake thermal conditions (*i.e.*, cold water temperatures,  $< 4.5^{\circ}\text{C}$ ; Bronte et al., 2017). Hatchery-produced fish can have lower fitness in natural environments than wild fish (Araki et al. 2008; Bailey et al. 2010; Christie et al. 2014). Offspring from parents haphazardly selected for artificial breeding and reared in captivity before release have the potential to induce strong directional selection and harm naturally recruiting populations (Araki & Schmid 2010; Tingley III et al. 2019). Transgenerational effect of lower larval performance and its potential effect on the response to selection are unknown but warrants investigation (Ford 2002; Araki et al. 2008; Araki & Schmid 2010; Christie et al. 2014). The consequences an artificial environment may have on the genetic diversity within a population and fitness of post-stocking individuals needs to be considered in ongoing restoration and conservation efforts (Tingley III et al. 2019).

Identifying the genetic mechanisms (*i.e.*, SNPs and gene expression) involved in the thermal adaptation and acclimation of coregonine populations is an important next step. Variation in certain genetic markers and survival under thermal stress may allow managers to determine the genotypes associated with increased survival at variable or increasing temperatures (Narum et al. 2013). Examining gene expression across populations and temperature treatments will help identify and evaluate the function of differentially expressed genes and potential physiological pathways that may be disproportionately under- or over-represented with thermal stress (Rougeux et al. 2018). Furthermore, the combination of genomic tools (*e.g.*, genome-wide association study and

RNA-seq) in thermal ecology experiments can provide valuable insight into the functional significance of markers associated with thermal tolerance (Rougeux et al. 2018). Considerable progress has been recently made in advancing our genomic knowledge of Laurentian Great Lakes coregonines that will provide a foundation for this work (Ackiss et al., 2020; Blumstein et al., 2020; Eaton et al., 2021; Lachance et al., 2021).

## **Conclusions**

The rapidity at which winter environments are changing has revealed our ‘blind spot’ for winter biology (Ozersky et al. 2021). The results presented here and elsewhere (Karjalainen et al. 2015; Karjalainen, Jokinen, et al. 2016; Stewart, Mäkinen, et al. 2021; Stewart, Vinson, et al. 2021a) focus on how coregonine reproduction may be impacted by a warming climate and suggest that while we have much to learn, the effects of warming winters will vary among populations and with the magnitude of warming. These results highlight the importance of integrating natural habitat preferences into stock propagation programs to ensure offspring are set up for success upon reintroduction. A challenge for managers and propagation facilities is to consider the impact embryo incubation conditions may have on larval survival and performance in relation to production targets. Additionally, propagation and stocking may accomplish the short-term restoration objective of supplementing wild populations, but other limiting factors (*e.g.*, habitat loss, anthropogenic disturbances, water quality, invasive species) also need to be addressed to achieve long-term population conservation and viability (Tingley III et al. 2019). Maximizing phenotypic variation and adaptability to changing conditions (*i.e.*, portfolio

effect; Schindler et al., 2015, 2010) is a strong consideration in restoration and conservation efforts. Embracing management strategies that foster increased early-life stage fitness could improve the ability of coregonines to cope with environmental change in the wild and aid in addressing recruitment bottlenecks.

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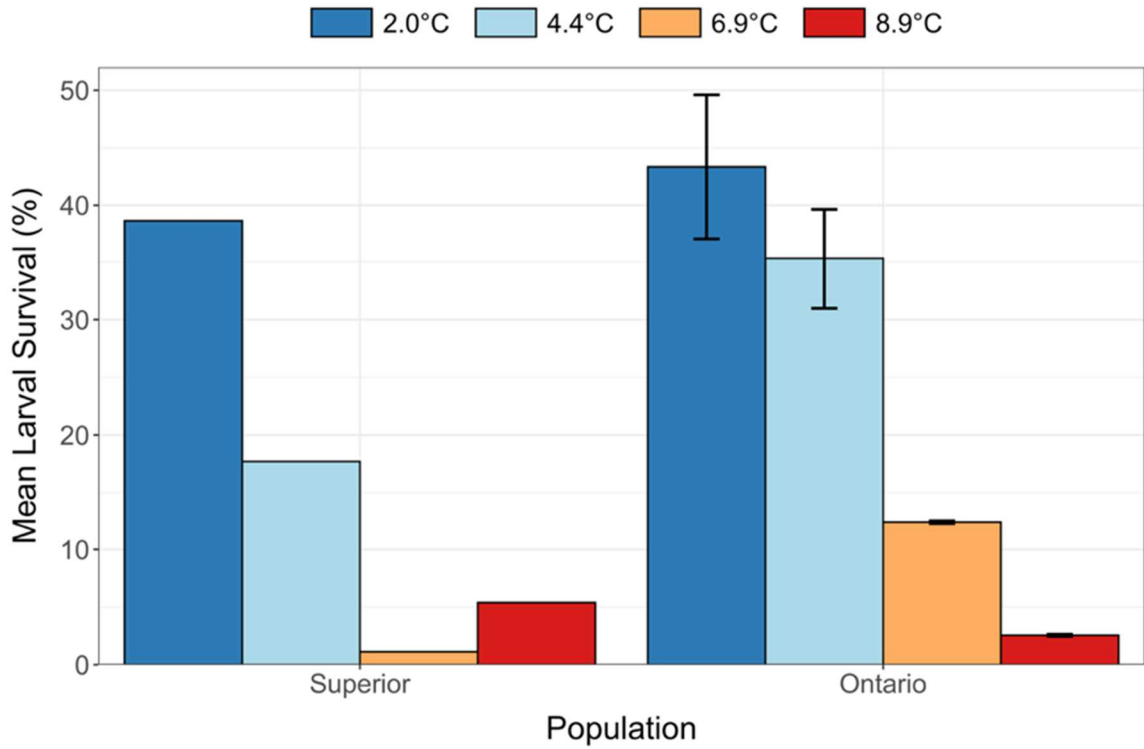


Figure 4.1: Mean larval survival (%) for larval cisco (*Coregonus artedi*) 60-days post-hatch from Lakes Superior and Ontario incubated at 2.0, 4.4, 6.9, and 8.9°C across replicate rearing tanks. Error bars indicate standard error. Lake Superior mean survival estimates are unreplicated and thus do not have error estimates.

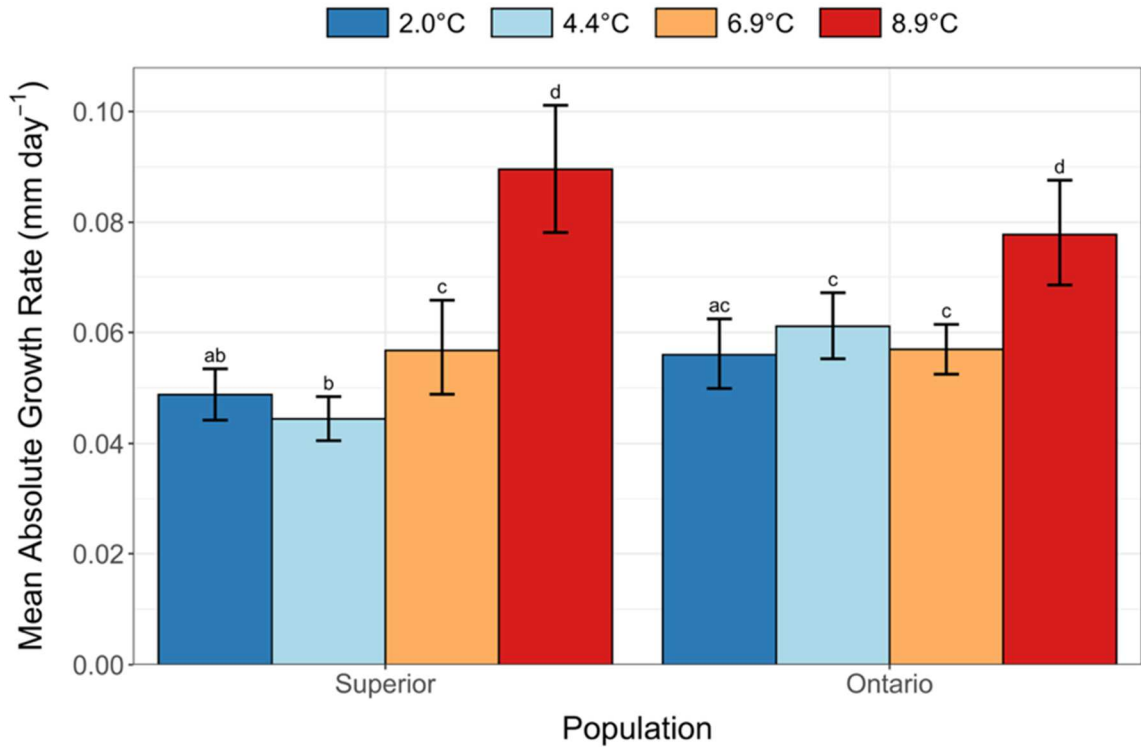


Figure 4.2: Mean absolute growth rates (mm day<sup>-1</sup>) for larval cisco (*Coregonus artedii*) 60-days post-hatch from lakes Superior and Ontario incubated at 2.0, 4.4, 6.9, and 8.9°C. Error bars indicate 95% bootstrapped confidence intervals. Letters indicate overlap of the observed mean absolute growth rate to the bootstrapped 95% confidence intervals of all pairwise comparisons.

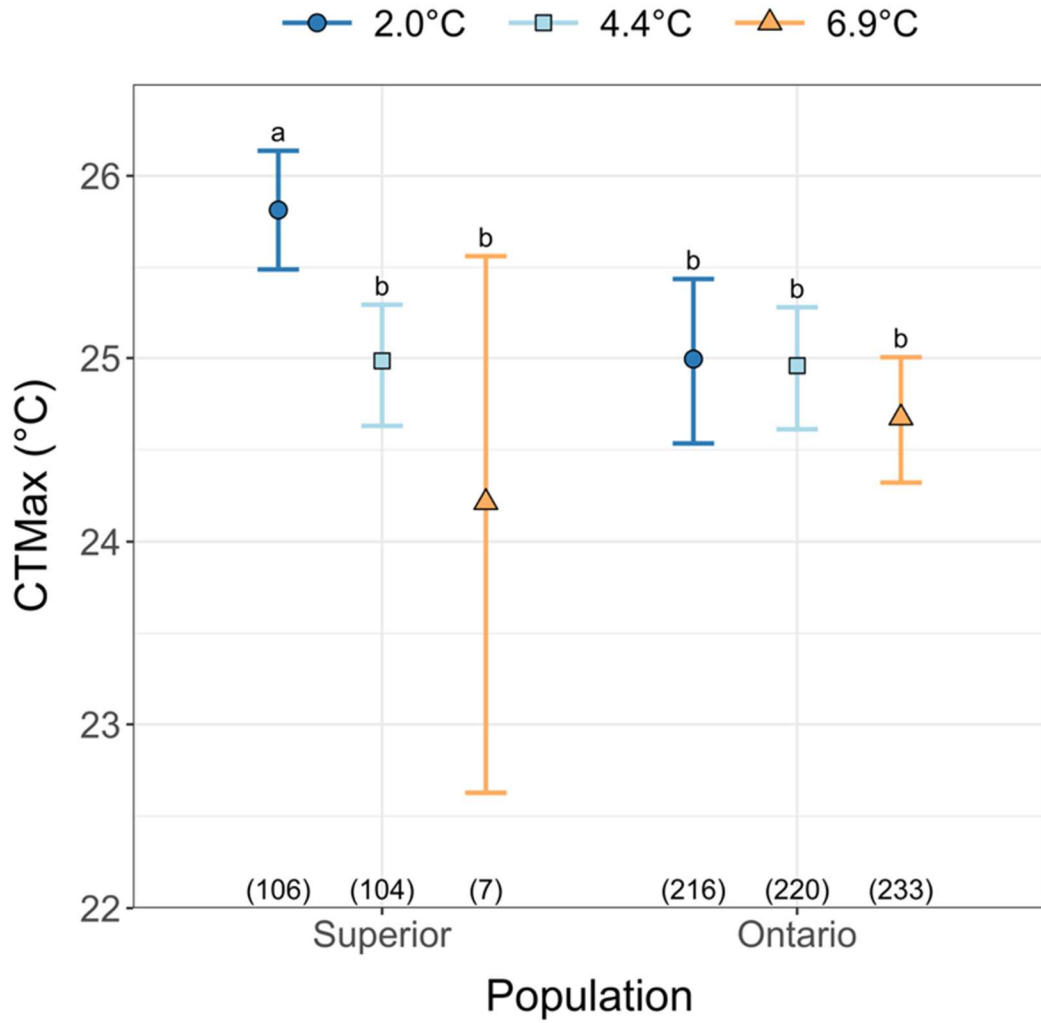


Figure 4.3: Critical thermal maxima (CTMax; °C) for larval cisco (*Coregonus artedii*) from lakes Superior and Ontario incubated at 2.0, 4.4, and 6.9°C. Error bars indicate 95% bootstrapped confidence intervals. Letters indicate overlap of the observed CTMax to the bootstrapped 95% confidence intervals of all pairwise comparisons. Sample sizes are indicated in parentheses.

**CHAPTER 5: WINTER IS NOT COMING: EVALUATING IMPACTS OF  
CHANGING WINTER CONDITIONS ON COREGONINE REPRODUCTIVE  
PHENOLOGY**

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## **Abstract**

Water temperature is a key driver in lakes that experience seasonality in climatic forcing because it has a fundamental effect on nearly all biological activities. Fishes in northern latitude lake ecosystems are at risk from climate-induced warming lake water temperatures because the strong seasonal pattern is degrading and the inability to evade warming habitats through migration. Consequently, observed responses of lacustrine fishes to climate-induced changes in thermal conditions include within-lake shifts in habitat distributions and shifts in phenology of life-history events. We developed temperature-dependent embryo development models for a group of cold, stenothermic fishes (Salmonidae Coregoninae) across the Laurentian Great Lakes and Europe to assess the potential impacts of climate-induced changes in water temperature. We simulated lakebed water temperatures for each study group and investigated changes in reproductive phenology across historic (1900-2006) and three future climatic-warming scenarios (2007-2099). Models predicted that climate-induced increases in water temperatures are likely to cause delayed spawning, shorter embryo incubation lengths, and earlier larval hatching. Relative changes increased as climate change scenarios increased in severity and were higher for lower-latitude populations compared to higher-latitude populations. Our simulations demonstrated that subtle changes in water temperature can translate into substantial changes in the reproductive phenology of coregonines among our study groups. We expect that the changes in coregonine reproductive phenology predicted by our models, in the absence of thermal adaptation,

will have negative implications for population sustainability throughout the current century, even under the lowest climate-emission scenario.

## **Introduction**

Warming lake temperatures worldwide (O'Reilly et al. 2015; Maberly et al. 2020) is an imminent threat to lacustrine fish (Dahlke et al. 2020). Unlike riverine or marine fishes, lacustrine fish are largely unable to evade warming habitats. The vulnerability of populations varies among lakes depending on the magnitude of thermal regime change and on species and life-stage specific temperature tolerances (Dahlke et al. 2020).

Holarctic fishes are predicted to be at risk because the strong seasonal pattern in northern latitude lake ecosystems is degrading (Winslow et al. 2017; Sharma et al. 2019; Maberly et al. 2020; Woolway et al. 2021), and their life history is innately linked to seasonal climate patterns (Winder & Schindler 2004). Disrupted seasonal patterns have resulted in positive feedback loops with warmer winter temperatures and shorter periods of winter ice coverage, earlier and rapid spring water warming, warmer and prolonged summer growing seasons and stratification periods, and delayed autumn cooling (Schindler et al. 1990; Sharma et al. 2019; Maberly et al. 2020; Woolway et al. 2021). These changes in seasonal temperatures and lake mixing have modified lake ecosystem productivity (O'Reilly et al. 2015; Yankova et al. 2017), which can have large impacts on ecosystem structure and function (Carpenter et al. 2011; Bhagowati & Ahamad 2019).

Most observed fish responses to climate-induced changes in thermal conditions are shifts in within-lake habitat distributions (Tunney et al. 2014; Guzzo et al. 2017) and seasonal timing of life-history events (Parmesan 2006; Farmer et al. 2015; Slesinger et al. 2021; Woods et al. 2021). Spawning adults and embryos are hypothesized to be the most temperature-sensitive life-stages in fishes based on the concept of limited

cardiorespiratory capacity and thermal tolerance (Dahlke et al. 2020). Warming waters will also shorten embryo incubation times resulting in earlier larval hatch dates (Reist et al. 2006; Karjalainen et al. 2015; Stewart, Mäkinen, et al. 2021). Fish reproductive strategies have generally evolved to account for seasonal changes in resources and allow for the most energy-intensive period of the consumer's reproductive phenology to align with the peak availability of prey resources (Hjort 1914; Cushing 1990; Lowerre-Barbieri et al. 2011; Lyons et al. 2015). The spatio-temporal synchrony between larval fish and their prey is believed to be an important driver of interannual variation in fish year-class strength (Cushing 1990; Nyberg et al. 2001; Straile et al. 2015).

Freshwater whitefish, Salmonidae Coregoninae (hereafter coregonines), is a group of cold, stenothermic fish species of high economic and ecological importance (Bogue 2001; Nyberg et al. 2001; Lynch et al. 2016). Over the past several decades, coregonine populations worldwide have experienced population declines and are the focus of reintroduction, restoration, and conservation efforts in many lakes across the northern hemisphere (Zimmerman & Krueger 2009; Anneville et al. 2015; Bronte et al. 2017). Population declines are related to low survival to age-1 (i.e., recruitment; Nyberg et al. 2001; Parks & Rypel 2018). Reasons for declining recruitment are unknown, but climate-induced increases in water temperatures during critical early-life stages is a leading hypothesis (Nyberg et al. 2001; Jeppesen et al. 2012; Anneville et al. 2015; Karjalainen et al. 2015).

Coregonines generally spawn near shore in late-autumn; embryos incubate under winter ice and hatch in spring near ice-out (Karjalainen et al. 2015; Eshenroder et al.

2016). For autumn-spawning coregonines, the seasonal decrease in water temperature initiates spawning and winter water temperature is positively related to embryo development rate and negatively related to incubation duration (Colby & Brooke 1973; Luczyński & Kirklewska 1984; Karjalainen et al. 2015; Eshenroder et al. 2016; Stewart, Mäkinen, et al. 2021). Climate change projections suggest that warming lake temperatures in autumn and winter could alter the timing of spawning and incubation time, and subsequent hatching time and survival of early-life stage coregonines (Nyberg et al. 2001; Karjalainen et al. 2015; Karjalainen, Jokinen, et al. 2016; Stewart, Vinson, et al. 2021a).

To further investigate how warming water temperatures may influence coregonine embryo development, we modeled the response of coregonine reproductive phenology to future climatic-warming scenarios for coregonine populations across North America and Europe. We hypothesized that delays in coregonine spawning, as a consequence of changes in autumn cooling, result in altered embryo incubation durations (i.e., number of days between spawning and hatching) and hatching times. Our predictions were that delayed cooling in autumn water temperature would cause delayed spawning times, with one of the following subsequent scenarios: (1) higher winter water temperatures, shortened incubation durations, and earlier hatching times, (2) normal winter water temperatures with shorter incubation durations and earlier hatching times, or (3) normal winter water temperatures and incubation durations with delayed hatching times. We expected coregonine populations that historically spawn at colder temperatures to have

higher relative changes in reproductive phenology as a result of climate warming compared to populations that historically spawn at warmer temperatures.

## Methods

We developed temperature-dependent embryo development models for eight coregonine study groups, validated newly fit models with existing *in situ* observations, developed lake bottom thermal regimes based on climatic-warming scenarios, and ran future simulations for study groups with validated models.

### *Study Locations and Species*

Study groups included cisco (*Coregonus artedi*) from two populations in Lake Superior [Apostle Islands (USA) and Thunder Bay (Canada)] and one in Lake Ontario (USA), vendace (*C. albula*) in Lake Southern Konnevesi (Finland), and European whitefish (*C. lavaretus*) in lakes Southern Konnevesi, Constance (Germany), Geneva (France), and Annecy (France; Table B.1).

### *Temperature-dependent Embryo Development Model Description*

Embryo development rates were expressed as the reciprocal number of days from fertilization to a given developmental stage (Colby & Brooke 1973; Luczyński & Kirklewska 1984; Eckmann 1987). The generalized equation relating rate of development to 50% hatching ( $DR_{50}$ ) with respect to incubation temperature ( $x$ ; °C) is

$$DR_{50} = ab^x c^{x^2}$$

where  $a$ ,  $b$ , and  $c$  are polynomial coefficients and the semilog form is

$$\log_{10} DR_{50} = \log_{10} a + x \log_{10} b + x^2 \log_{10} c$$

$DR_{50}$  models for cisco from lakes Superior and Ontario and vendace from Lake Southern Konnevesi were fit with experimental incubation duration data on embryos incubated at constant water temperatures of *ca.* 2.0, 4.5, 7.0, and 9.0°C (Stewart, Mäkinen, et al. 2021; Table 5.1). Additional models were fit for littoral spawning morphotypes of European whitefish from Lake Geneva using embryo incubation data (unpublished data, EL and CG). Winter temperatures normally decline to only 5-7°C in these two lakes, so only two incubation temperatures were evaluated (contemporary at 7.0°C and warmer winters at 9.0°C). Thus, only linear models were fit. The semilog form (i.e.,  $\log_{10}DR_{50}$ ) was fit to obtain model coefficients for each study group using the mean within-family number of days from fertilization at each incubation temperature. Furthermore, published  $DR_{50}$  models were used for the littoral and pelagic spawning morphotypes of European Whitefish (*C. lavaretus macrophthalmus* and *C. lavaretus wartmanni*, respectively) from Lake Constance, vendace from Lake Kosno (Poland), and cisco from Pickerel Lake (USA; Colby and Brooke, 1973; Eckmann, 1987; Luczyński and Kirklewska, 1984; Table 5.1). Hereafter,  $DR_{50}$  models we fit to each study group from experimental data (Stewart, Mäkinen, et al. 2021; unpublished data, EL and CG) are referred to as population-specific models while  $DR_{50}$  models with published polynomial coefficients for species outside of our study groups (Colby and Brooke, 1973; Eckmann, 1987; Luczyński and Kirklewska, 1984) are species-specific models.

To predict development time to 50% hatching,  $\log_{10}DR_{50}$  was calculated for each daily mean temperature since spawning and the antilog<sub>10</sub> taken to estimate the daily

proportion of development. When the cumulative daily proportions of development equaled one, 50% hatching was assumed to have occurred.

#### *Data Sources*

Fishery-dependent spawning data were available for lakes Superior (Apostle Islands and Thunder Bay) and Annecy (Table B.2). Commercial fishers from lakes Superior and Annecy used gillnets to target spawning aggregations and recorded date, sex, maturity, and gonad condition from a subset of their catch (e.g., first 10 fish; Yule et al. 2008).

Fishery-independent spawning data collected during spawning surveys or broodstock collections were available for lakes Southern Konnevesi, Geneva, and Ontario (Table B.2). Spawning adults were collected using gillnets for lakes Southern Konnevesi and Geneva and trap nets for Lake Ontario at known spawning times and locations. Spawning adults collected were either assessed for gonad condition (i.e., green, ripe, spent) if actively spawning or were transported and held in hatchery ponds fed by lake water until spawning was observed; data provided daily distributions of spawning intensity. Daily number of ripe spawning individuals was reported for Lake Geneva, while daily gonad condition was reported for lake Southern Konnevesi and Ontario.

Repeat larval abundance data (i.e., *ca.* weekly) were gathered for each study group to estimate dates of hatching (Table B.2). Larval collections were made by either a seine or plankton net through ice, or along the surface or at a stratified depth when lakes were ice-free (Perrier et al. 2012; Karjalainen et al. 2019; Lucke et al. 2020; McKenna et al. 2020). All larvae collections began prior to the start of hatching or with low

abundance so the date of first capture was assumed to be the start hatch date, except for the Lake Superior (Apostle Islands) and Lake Geneva study groups. Larvae from Lake Superior (Apostle Islands) were sampled on fixed dates annually, presumably during or after peak hatching, and thus the hatch date of individual larvae were back-calculated from total lengths assuming an absolute growth rate of  $0.18 \text{ mm day}^{-1}$  (Oyadomari & Auer 2007) and a length-at-hatch of 9.9 mm (Stewart, Mäkinen, et al. 2021). No larval growth data were available to back-calculate hatch dates for Lake Geneva so capture dates were assumed to be hatch dates.

Daily lakebed winter water temperatures were obtained from deployed temperature loggers (e.g., HOBO® Water Temperature Pro v2) for lakes Superior (Apostle Islands), Ontario, Southern Konnevesi, Geneva, and Annecy on known spawning habitat or depth (Table B.2). Only a single winter (2017-18) of lakebed temperature data were available from Chaumont Bay, Lake Ontario, and thus we compared water temperatures from satellite surface water (<https://podaac.jpl.nasa.gov/MEaSURES-MUR>) and U.S. Geological Survey Oswego River gauge (gauge number 04249000) to the observed lakebed winter water temperatures from Chaumont Bay in 2017-2018. The Oswego River gauge provided the closest representation of the lakebed thermal conditions of Chaumont Bay (mean daily difference =  $0.77^{\circ}\text{C}$ ) and was used as the *in situ* winter water temperatures for the Lake Ontario study group. Daily lakebed winter water temperatures for Lake Superior (Thunder Bay) were provided by the City of Thunder Bay Bare Point Water Treatment

Plant, which measures water temperature at intake pipes submerged 733 m from shore at 13-m depth.

### *Model Validation*

Population-specific  $DR_{50}$  models fit from experimental incubation duration data (Stewart, Mäkinen, et al. 2021; unpublished data, EL and CG) were tested using *in situ* daily lakebed winter water temperatures to compare model outputs (i.e., hatching dates) to the observed hatching data from eight coregonine study groups across North America and Europe. Experimental data were not available to fit population-specific models for lakes Annecy and Superior (Thunder Bay), thus the population-specific model from closely-related study groups and lakes were. We therefore used our models from Lake Geneva to Lake Annecy and from Apostle Islands in Lake Superior to Thunder Bay.

Initiation and completion of contemporary spawning was based on observed water temperatures. Coregonine spawning data to calculate the spawning temperatures were either 1) the daily proportion of ripe females leading to spawning or 2) the daily number of spawning individuals on spawning grounds. The onset of spawning was assumed to start on the date when either >10% of females captured daily were ripe or when the number of daily spawners was >10% of the total number of spawning individuals annually. The end of spawning was calculated as the nearest date to the start of spawning when either <10% of females were ripe or when the number of daily spawners was <10% of the total number of spawning individuals annually. If the end of spawning period could not be calculated (e.g., commercial roe fishery ceased once eggs were free flowing), we assumed the spawning period ended 9 days after the start of spawning (Straile et al.

2015). The water temperatures from the first and last date of the spawning period were taken from *in situ* daily lakebed winter water temperatures and averaged across all years available to define contemporary start and ending spawning water temperatures. If the years with spawning data did not overlap the years with water temperature data, the mean starting and ending days of year for the spawning period were calculated from all years of available spawning data, and the water temperatures at each mean starting and ending spawning days of year were averaged across all available water temperature years. For Lake Constance, where the dominant form of European whitefish spawn in pelagic water and embryos sink to a depth of 200-250 m (Straile et al. 2007), the spawning start dates were calculated using published equations from the date that the upper 10-m of the water column reached 10°C isothermal conditions and spawning was assumed to end after 9 days (Straile et al. 2015).

To validate the models for each study group, the mean spawning date was estimated from the calculated spawning start and end water temperatures for each year of available *in situ* water temperature data. The predicted development time to 50% hatching was calculated using daily water temperatures, beginning at the mean spawning date, for each population-specific model.

Mean observed hatching days of year were calculated as a weighted mean with daily larval abundance as the weight across all years available for each study group (Figure 5.1). The mean degree-days at hatching from the population-specific models we fit and the respective species-specific models from literature were compared to the mean observed degree-days at hatching for each study group (Colby & Brooke 1973;

Luczyński & Kirklewska 1984; Eckmann 1987). A model was considered validated if the difference between the model degree-days at hatching and the mean observed degree-days at hatching was within  $\pm 50^{\circ}\text{C}$ , and the closest validated model (i.e., either the population-specific model or species-specific model) to the mean observed degree-days at hatching was selected for each study group.

### *Climate-scenarios*

Daily lake bottom water temperatures were simulated within the Inter-Sectoral Impact Model Intercomparison Project phase 2b (ISIMIP2b) local lake sector (Warszawski et al. 2014), using the SimStrat v2.1 lake model (Gaudard et al. 2019) for years 1900-2099. To drive the lake model, EWEMBI bias-corrected (Lange 2019) climate model projections from ISIMIP2b were used, specifically projections from GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-LR, and MIROC5 for historic (1900-2006) and future periods (2007-2099) under three representative concentration pathways (RCP): RCP 2.6, 6.0, and 8.5. These pathways included a range of potential future global radiative forcing with RCP 2.6 the lowest-emission scenario and RCP 8.5 the highest-emission scenario (IPCC 2014).

To simulate how warming water temperatures would manifest in each of our study groups, we used lakes from ISIMIP as case studies. A total of 59 modeled case-study lakes from ISIMIP were categorized into climate zones following the definitions of Maberly et al. (2020) and maximum depth zones of 0-10, 10-25, 25-50, and 50+ m. Water temperatures from case-study lakes were averaged across all four climate model projections by each date, climate zone, and depth category to provide a simulated daily

estimate of thermal spawning habitat for each climate zone and lake depth category combination. Each study group was assigned by climate zone and typical coregonine spawning depth, and the respective simulated mean daily water temperatures were used for each study group. Only 19 of the 59 available case-study lakes matched the climate zone and depth categories of our study groups and were used (Table B.1).

Lakes Geneva and Annecy are deep, peri-alpine lakes where coregonine spawning occurs in shallow waters (<5 m). The contemporary thermal spawning habitat for these two lakes were not well represented by the simulated bottom water temperature scenarios. Lakes Geneva and Annecy were available as modeled case-study lakes through ISIMIP and thus the lake-specific simulated daily water temperatures at the 5-m depth stratum were used, instead of the bottom water temperatures (mean maximum depth = 196 m), as the thermal scenarios for these lakes.

#### *Model Simulations*

In the model, for each simulated year, spawning began on the first day that the 5-day running average of simulated water temperatures dropped below the population-specific start spawning temperature and ended on the first day that the 5-day running average of simulated water temperatures dropped below the population-specific end spawning temperature. Eggs were deposited throughout the defined spawning period according to the proportional rate of daily water temperature change, where larger daily decreases in temperature resulted in higher daily spawner abundances, assuming 500 female spawners annually and each female deposited 100 eggs to provide a relative index of cohort size. If the simulated water temperatures did not decrease sufficiently to end

spawning, we assumed spawning ended after 20 days. Daily cohorts of deposited eggs were run through the respective validated  $DR_{50}$  model for each study group, and the hatch date was estimated. Daily hatch cohort size was determined using embryo survival estimates from Stewart et al. (2021) and unpublished data (EL and CG). Linear models were fit to the embryo survival estimates from the incubation temperature treatment range that the mean simulated incubation temperature was within (Table B.3), and the linear model predicted the embryo survival estimate for the simulated mean incubation temperature. The predicted embryo survival percentage was applied to each daily cohort of spawned embryos to determine the daily number of embryos successfully hatched.

To estimate the magnitude of change in reproductive phenology, we calculated the incubation duration for each simulated embryo and mean spawning and hatching dates for each study group across historic (1900-2005) and future periods (2006-2099). Mean spawning date, incubation duration, and hatch date anomalies were calculated as deviations from the respective mean trait value during the historical period (1900-2005) for each study group, future year, and RCP scenario. Linear regressions were fit through simulated years to trait anomalies for each study group and RCP scenario. The linear models of the trait anomalies for each RCP scenario were compared using a two-way analysis of variance within each study group and subsequent Tukey post-hoc test if a significant difference among slopes was found ( $\alpha = 0.05$ ).

All simulations and analyses were performed in R version 4.0.5 (R Core Team 2021).

## **Results**

Our population-specific models were fit, validated, selected for cisco from lakes Superior (Apostle Islands) and Ontario and vendace from Lake Southern Konnevesi (Tables 5.1 and 5.2). The species-specific model was validated and selected for European whitefish from Lake Annecy (Eckmann 1987). No model was validated for cisco from Lake Superior (Thunder Bay) and European whitefish from lakes Southern Konnevesi and Geneva, and thus results are not reported for these study groups (Tables 5.2).

Study groups with validated  $DR_{50}$  models displayed variable development rates among study groups but were similar within species across populations (Figure 5.2).  $DR_{50}$  models for European whitefish from Lake Constance (and applied to Lake Annecy) had the fastest development rates while models for vendace from Lake Southern Konnevesi had the slowest embryo development rates. The rate of embryonic development decreased with increasing latitude (Figure 5.2).

### *Spawning*

Model simulations predicted that spawning will be delayed as climate change scenarios increase water temperatures for all study groups except Lake Constance European whitefish (Figures 5.3 and 5.4). The RCP 8.5 scenario resulted in the greatest deviation from the mean historical spawning time in all study groups (mean increase = 0.36 days year<sup>-1</sup>). Spawning time of European whitefish from Lake Annecy had the largest response to increased temperature (1.01 days year<sup>-1</sup>), and the RCP 6.0 and 8.5 scenarios resulted in skipped spawning years and the complete absence of adequate thermal habitat required to initiate spawning by 2084 and 2049, respectively (Figure 5.4). Cisco from lakes Superior and Ontario and vendace from Lake Southern Konnevesi had

similar delayed spawning responses to increased temperatures within each RCP scenario (Figure 5.3). Spawning time of European whitefish from Lake Constance responded similarly among RCP scenarios and had minimal change from historical spawning times ( $< 0.07$  days year<sup>-1</sup>; Figure 5.4). All RCP anomaly slope pairwise comparisons were significantly different for spawning date within each study group ( $p < 0.05$ ), except for vendace from Lake Southern Konnevesi between RCP 2.6 and 6.0 ( $p = 0.060$ ; Figure 5.5).

### *Incubation Length*

Embryo incubation lengths (i.e., number of development days) were predicted to decrease as a result of increased water temperatures from climate change for all study groups examined (Figures 5.3 and 5.4). The greatest deviation in incubation length from the mean historical incubation length was the RCP 8.5 scenario for all study groups (mean decrease =  $0.37$  days year<sup>-1</sup>). Incubation length had similar responses within the RCP 8.5 scenario to increased temperatures among all study groups, with vendace from Lake Southern Konnevesi having the greatest response ( $-0.41$  days year<sup>-1</sup>) and European whitefish from Lake Constance the smallest response ( $-0.23$  days year<sup>-1</sup>; Figures 5.3 and 5.4). Furthermore, all study groups responded similarly to increased temperatures within the RCP 6.0 and 2.6 scenarios (mean =  $-0.17$  and  $-0.04$  days, respectively). All RCP anomaly slope pairwise comparisons were significant for incubation length within each study group ( $p < 0.05$ ; Figure 5.5).

### *Hatching*

Model simulation outputs for hatching date were variable among study groups (Figures 5.3 and 5.4). Hatching dates of cisco from Lake Ontario, vendace from Lake Southern Konnevesi, and European whitefish from Lake Constance were earlier in response to increased temperatures, while hatching dates of European whitefish from Lake Annecy were later and did not change for cisco from Lake Superior as water temperatures increased. The hatching date anomaly slopes among RCP scenarios were not significantly different for cisco from Lake Superior ( $p = 0.949$ ). All RCP anomaly slope pairwise comparisons were significant for vendace from Lake Southern Konnevesi, while comparisons between RCP 2.6 and 6.0 for Lake Ontario cisco ( $p = 0.259$ ) and Lake Constance European whitefish ( $p = 0.102$ ) and between RCP 6.0 and 8.5 for Lake Annecy European whitefish ( $p = 0.147$ ) were not significant. All other comparisons were significant ( $p < 0.05$ ; Figure 5.5).

## **Discussion**

Our hypothesis that delays in coregonine spawning, as a consequence of changes in autumn cooling, would result in altered embryo incubation durations (i.e., number of days between spawning and hatching) and hatching times was supported for all study groups. Simulation models predicted that climate-induced increases in water temperatures will shift reproductive phenology of coregonines causing (1) delayed spawning, (2) shorter embryo incubation durations, and (3) earlier larval hatching. Relative changes were higher with more severe climate change scenarios and at lower latitudes where embryos have higher contemporary incubation water temperatures.

In our simulations, the timing and number of spawning days were regulated by when, and in some instances if, water temperatures cooled to provide adequate spawning conditions. Oocyte development in fish is driven by energy content and is relative to water temperature during the germ-cell-developing season, and final oocyte maturation is a prerequisite for successful fertilization (Nagahama & Yamashita 2008; Burt et al. 2011; Im et al. 2016). Elevated summers and autumn temperatures could place additional energy demands on adults and require longer feeding periods later into autumn. By shifting spawning to allow for extended feeding and to align with cooler water temperatures, coregonines could mitigate the disproportionate energy demand during the summer when metabolic rates are higher. Spawning at suboptimal water temperatures has the potential to induce considerable fertilization failure or embryo mortality if gametes are not adequately mature prior to spawning (Burt et al. 2011). The pre-fertilization thermal environment can also have intergenerational effects and shape offspring phenotypes, and thermally stressful spawning conditions can reduce the size and swimming performance in European whitefish larvae (Kekäläinen et al. 2018). Thus, delayed spawning could be a more efficient long-term life-history strategy for population persistence than the time-intensive evolutionary process of adults and embryos adapting to increased temperatures.

Shifting reproductive timing is a plausible response to warming temperatures. Contemporary coregonine populations exhibit multiple spawning strategies ranging from autumn to spring-spawning stocks (Eronen & Lahti 1988; Hénault & Fortin 1991; Schulz et al. 2006; Ohlberger et al. 2008). Thermal habitat used by high-latitude or deep-

spawning populations could be less affected by climate change and may still provide adequate thermal spawning and incubation conditions if water temperatures continue to rise, compared to low-latitude or littoral-spawning populations. For example, Lake Annecy is near the southern native extent for European whitefish and had the largest shift in spawning time among our study groups, but adequate thermal spawning temperatures were absent by the middle of the current century under the worst-case climate scenario. This projection is likely to be applicable for populations within the same geographic region that have similar lake morphology and thermal condition where we were not able to validate a population-specific  $DR_{50}$  model (i.e., Lakes Geneva; Berthon et al. 2013; Jacquet et al. 2014), and even more dire projections could be expected for non-native populations south of Lake Annecy [e.g., Lake Garda (Italy); Volta et al. 2018]. However, these southern European lakes are deep (> 80 m) with stable thermal refugia outside of the littoral zone (Kelly et al. 2020). Shifting spawning strategies to use deep, thermal refugias could provide adequate thermal conditions for ovulation to initiate, but whether suitable coregonine spawning habitat is available and level of oxygen sufficient is unknown (Jane et al. 2020; Kelly et al. 2020).

A portfolio of spawning strategies across environmental gradients may be key for future fish population sustainability (Burt et al. 2011; Schindler et al. 2015; Aplet & McKinley 2017; Thompson et al. 2020). Coregonine spawning stocks which possess high genetic diversity and phenotypic plasticity in life-history traits may be better suited to use a wide range of spawning habitats (Karjalainen, Urpanen, et al. 2016; Pauflve 2019), and may contribute differentially to offspring performance and recruitment (Luck et al. 2003;

Figge 2004). Parental effects can induce variability in phenotypes and provide more flexibility in offspring to cope with changing inter-annual environmental conditions, prevent full year-class failure, and ensure population persistence (Wright & Trippel 2009; Oomen & Hutchings 2015).

Spawning scenarios determined the majority of the changes in reproduction phenology but embryos are static and unable to evade changes in winter water temperatures post-spawning (Stockwell et al. 2014). Elevated incubation water temperatures accelerated embryo rates of development and hatching time in our simulations and were not negated by delayed spawning. The frequency of shorter, warmer winters is projected to increase (Sharma et al. 2019), which corresponds with our simulation results suggesting future incubation durations will decrease across all study groups. In the absence of changes to spawning behavior or habitat, warmer and shorter incubations could cause higher coregonine embryo and larvae mortality, increased occurrence of embryo deformities, and smaller and less robust larvae at hatching compared to cold, long incubations (Stewart, Mäkinen, et al. 2021; Stewart, Vinson, et al. 2021b). Additionally, reduced ice formation caused by warmer air and water temperatures could also decrease cisco lengths-at-hatching (Stewart, Vinson, et al. 2021a). A complex mix of environmental factors during embryogenesis can modify the fitness of larvae and generate high variability in fish year-class strength (Hjort 1914; Houde 1989b; Marjomäki 2004; Figure 5.6).

Coregonine populations where embryos incubate in cold littoral waters (< 4°C) are hypothesized to rely on ice-break up and spring warming to trigger final embryo

development stages and hatching (Karjalainen et al. 2015). The rapid increase in spring water temperatures also synchronizes other phenological processes such as the onset of spring plankton blooms (Sommer et al. 2012). Our simulations suggest significant changes in length of incubation and subsequent hatching times, and changes in thermal regimes and time of hatching may result in temporal separation between coregonine larvae and their zooplanktonic prey. Increases in seasonal temperature variability could also cause mismatches with larval zooplankton prey if temperature changes are not heterogeneous across seasons (e.g., a cold winter followed by a warm spring; Straile et al. 2015).

The reduction in incubation duration may have a surprising benefit. Incubating embryos are vulnerable to predation (Stockwell et al. 2014) and warmer winter temperatures may influence standard metabolic rates of predators (Brett 1979; Brown et al. 2004). Coregonine embryos provide a lipid- and energy-rich diet item in winter when lake productivity is low, do not impose gape limitations to most predators, and do not induce pursuit costs typical of mobile prey. Benthic predators could intensify foraging on embryo to counteract higher energetic costs associated with increased winter water temperatures (Shuter et al. 2012). Thus, the decreased incubation duration and higher embryo development rates could shorten the period of vulnerability to benthic predators.

Fish year-class strength is largely dependent on larvae surviving from hatch through the first three to six months of life and successfully transitioning from endogenous to exogenous feeding (Hjort 1914; Houde & Hoyt 1987; Cushing 1990). Numerous size-dependent processes strongly influence when larvae need to first feed and

their ability to successfully forage (Miller et al. 1988). Coregonine larval body size at hatching is inversely related to incubation water temperature, and length-at-hatch and yolk-sac volume have a negative relationship (Karjalainen et al. 2015; Stewart, Mäkinen, et al. 2021). Warmer incubations result in coregonine larvae hatching earlier with smaller lengths and larger yolk-sacs (Stewart, Mäkinen, et al. 2021). Increased yolk-sac energy reserves at hatching may help larvae reduce starvation risk but the rate of endogenous feeding (i.e., yolk consumption) is regulated by metabolic demand (Kamler 2008). Earlier and warmer spring water temperatures in nursery zones, which induce earlier hatching, could accelerate yolk consumption in newly-hatched larvae and counteract the physiological trade-off between length-at-hatching and yolk-sac volume. Larvae hatching earlier in the spring may also have reduced swimming abilities, visual acuity, and more gape limitations, which can impact their ability to evade predators and forage efficiently (Miller et al. 1988; Myers et al. 2014). The physiological stress response of hatching earlier and the impact warming nursery water temperatures may have on yolk conversion efficiency is a logical and necessary next step to build on our simulation results.

Our models extend earlier approaches (Colby & Brooke 1973; Luczyński & Kirklewska 1984; Eckmann 1987) by incorporating mechanistic relationships to future climate-change scenarios from a wider range of populations. Because coregonines are highly developmentally plastic and exhibit diverse spawning behaviors (Muir et al. 2013), the transferability of published models to other populations appears inappropriate and likely to not represent population-specific characteristics well. The need for high-quality *in situ* reproductive and embryo development data is critical to fitting and

validating new populations-specific development models. For example, hatching data for European whitefish in Lake Geneva was only available for a single year with a limited sampling period and likely did not capture the start of hatching. This led to development models underestimating hatching when, in reality, the *in situ* data likely did not represent the true hatching period and created a limitation in our modeling efforts. Increasing field sampling efforts around these critical life stages will benefit future research and climate-change predictability, for both applied- and modeling-based methods.

Our simulations demonstrated that subtle changes in water temperature can translate into substantial changes in the reproductive phenology of coregonines among our study groups. Long-term changes in environmental conditions during reproductive and development periods could play a large role in generating variability in offspring success (Houde & Hoyt 1987; Little et al. 2020). The results of our modeling efforts highlight how water temperature is fundamental in regulating biological and physiological processes, but the impact of these changes is difficult to decipher as coregonines are behaviorally and developmentally plastic (Muir et al. 2013; Karjalainen et al. 2015). Quantifying the relationship between water temperature and coregonine reproductive phenology across a wide range of populations will be a useful tool for managers to determine what populations may be more susceptible to the consequences of climate change. We expect that the changes in coregonine reproductive phenology predicted by our models, in the absence of thermal adaptation, will have negative implications for population sustainability throughout the current century, even under the lowest climate-emission scenario.

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Table 5.1: Development rate equations to 50% hatching  $DR_{50}$  for cisco (*Coregonus artedi*) from lakes Superior, Ontario, and Pickerel, vendace (*C. albula*) from lakes Kosno and Southern Konnevesi, and European whitefish (*C. lavaretus*) from lakes Constance and Geneva. Population-specific  $DR_{50}$  models were fit to data for *C. artedi* from lakes Superior and Ontario, *C. albula* and *C. lavaretus* from Lake S. Konnevesi (Stewart, Mäkinen, et al. 2021), and *C. lavaretus* from Lake Geneva (unpublished data, EL and CG). Species-specific  $DR_{50}$  models were taken for *C. artedi* from Pickerel Lake (Colby & Brooke 1973), *C. albula* from Lake Kosno (Luczyński & Kirklewska 1984), and *C. lavaretus* (pelagic and littoral) from Lake Constance (Eckmann 1987). The coefficient of determination ( $R^2$ ) was provided for models fit in this paper and whether or not they were validated (see Table 5.2). All coefficients are in common logarithm ( $\log_{10}$ ), and coefficients from Eckmann (1987) were transformed from natural logarithm.

Model Group	Species	$\log_{10}DR_{50} =$	$R^2$	Validated
Lake Superior	<i>C. artedi</i>	$-2.3289 + 0.0717x - 0.0001x^2$	0.97	Yes
Lake Ontario	<i>C. artedi</i>	$-2.3836 + 0.0643x + 0.0008x^2$	0.98	Yes
Pickerel Lake	<i>C. artedi</i>	$-2.4088 + 0.0720x + 0.0011x^2$	--	--
Lake Kosno	<i>C. albula</i>	$-2.3035 + 0.0651x + 0.0004x^2$	--	--
Lake S. Konnevesi	<i>C. albula</i>	$-2.3664 + 0.0088x + 0.0050x^2$	0.94	Yes
Lake S. Konnevesi	<i>C. lavaretus</i>	$-2.4183 + 0.0459x + 0.0032x^2$	0.96	No
Lake Constance	<i>C. lavaretus</i> (littoral)	$-2.3002 + 0.1104x - 0.0031x^2$	--	--
Lake Constance	<i>C. lavaretus</i> (pelagic)	$-2.2419 + 0.1104x - 0.0033x^2$	--	--
Lake Geneva	<i>C. lavaretus</i>	$-2.1159 + 0.0528x$	0.86	No

Table 5.2: Model validation results for population-specific development to 50% hatching models ( $DR_{50}$ ) for cisco (*Coregonus artedi*) from lakes Superior (Apostle Island and Thunder Bay) and Ontario, vendace (*C. albula*) from Lake Southern Konnevesi, and European whitefish (*C. lavaretus*) from lakes Geneva and Annecy. Starting and ending spawning temperatures ( $^{\circ}\text{C}$ ) used as model parameters are listed and the model output (i.e., degree-days at hatching) from population-specific and species-specific models were compared to *in situ* hatching data for each study group. N indicates the number of available years with daily *in situ* water temperatures and that spawning temperatures were averaged across. Bolded degree-days at hatching indicates the selected  $DR_{50}$  model for each study group. Population-specific  $DR_{50}$  models were fit to data for *C. artedi* from lakes Superior and Ontario, *C. albula* and *C. lavaretus* from Lake S. Konnevesi (Stewart, Mäkinen, et al. 2021), and *C. lavaretus* from Lake Geneva (unpublished data, EL and CG). Species-specific  $DR_{50}$  models were taken for *C. artedi* from Pickerel Lake (Colby & Brooke 1973), *C. albula* from Lake Kosno (Luczyński & Kirklewska 1984), and *C. lavaretus* (pelagic and littoral) from Lake Constance (Eckmann 1987).

Study Group	Species	Spawning Temperatures		Mean Degree-days at Hatching			
		Start	End	Observed	Pop. Model	Species Model	N
Lake Superior (Apostle Islands)	<i>C. artedi</i>	4.3	3.0	250.1	<b>255.7</b>	335.0	3
Lake Superior (Thunder Bay)	<i>C. artedi</i>	4.9	4.4	452.3	337.9	405.3	4
Lake Ontario	<i>C. artedi</i>	4.1	2.7	377.5	<b>359.8</b>	344.1	10
Lake S. Konnevesi	<i>C. albula</i>	7.4	5.6	390.7	<b>439.0</b>	269.4	3
Lake S. Konnevesi	<i>C. lavaretus</i>	6.0	4.7	292.5	395.7	200.6	3
Lake Geneva	<i>C. lavaretus</i>	8.0	6.6	663.5	375.9	333.0	12
Lake Annecy	<i>C. lavaretus</i>	6.2	5.9	316.5	349.0	<b>331.0</b>	2

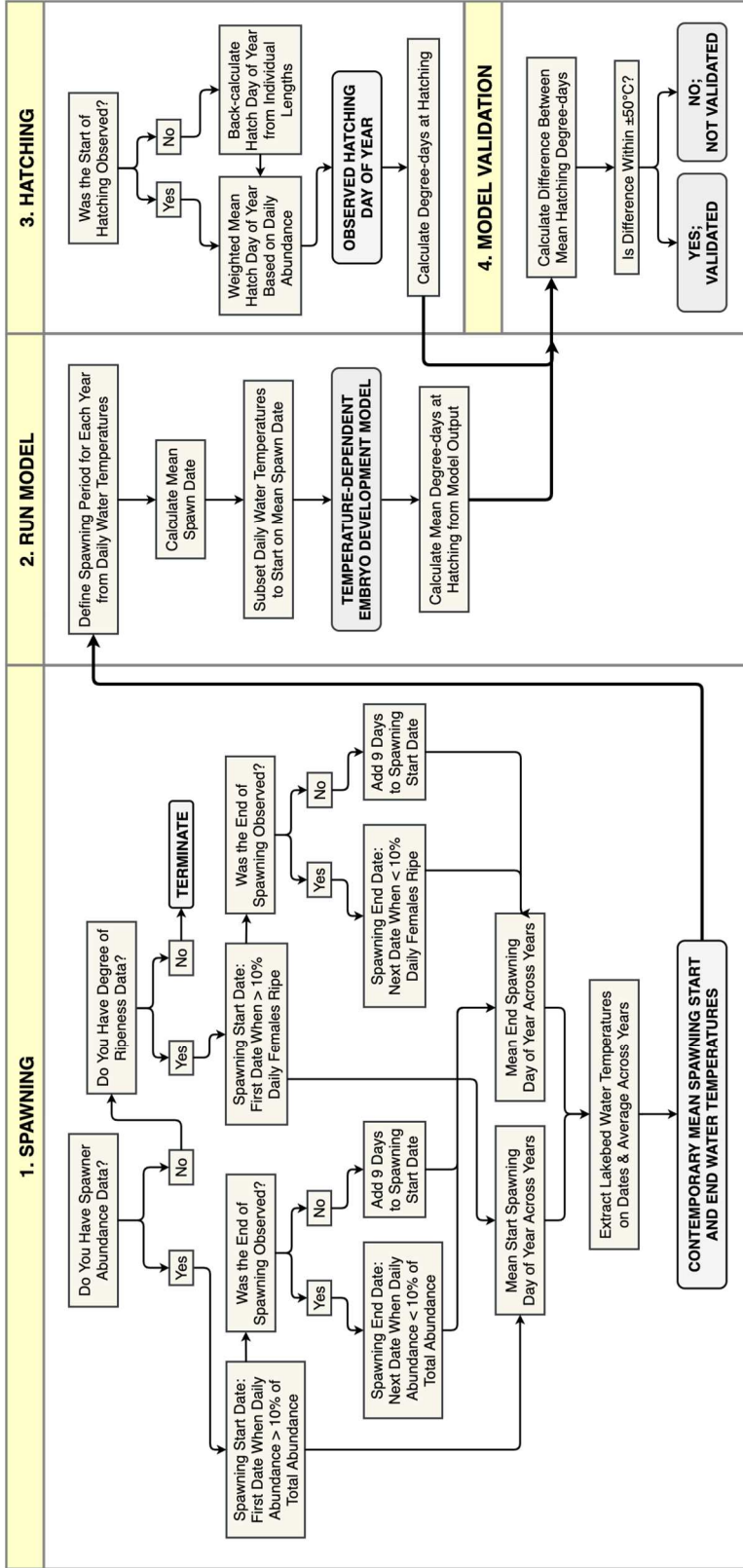


Figure 5.1: Workflow diagram describing the use of *in situ* spawning, hatching, and daily lakebed water temperature data in the model validation process.

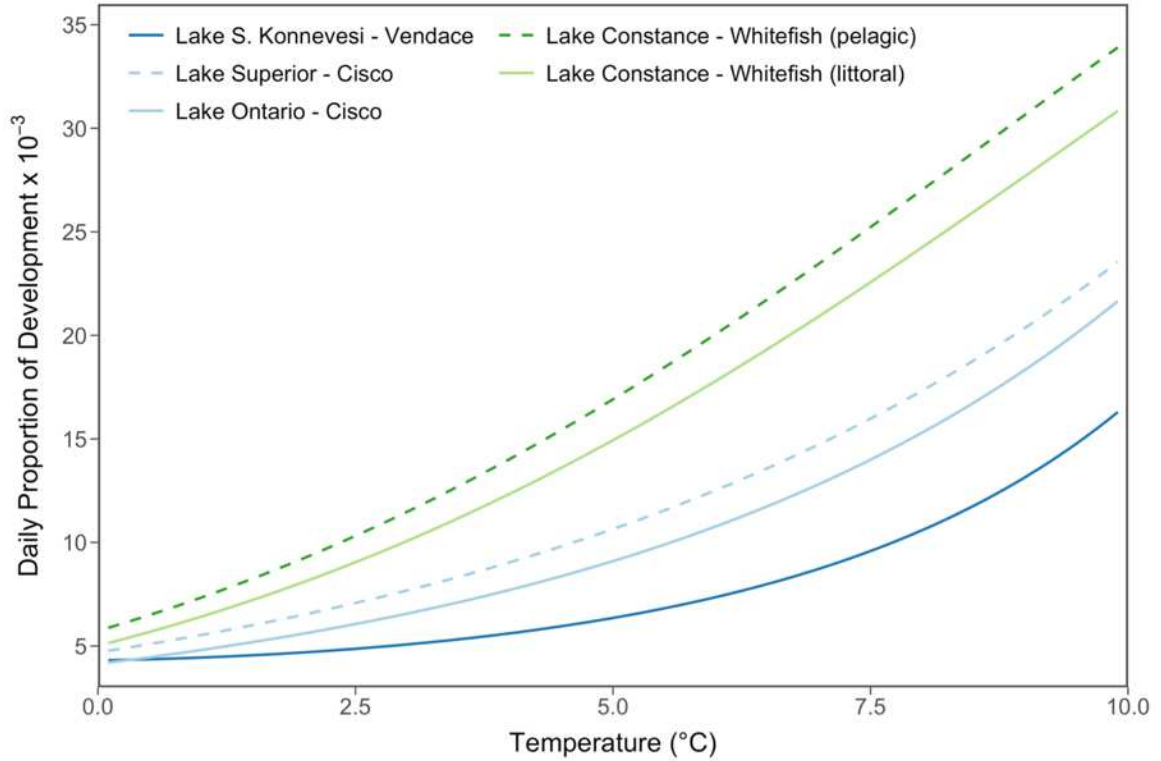


Figure 5.2: Predicted daily proportion of embryo development at water temperatures ( $^{\circ}\text{C}$ ) from validated development to 50% hatching ( $DR_{50}$ ) models for vendace (*Coregonus albula*) from Lake Southern Konnevesi, cisco (*C. artedi*) from lakes Superior and Ontario, and European whitefish (*C. lavaretus*) from Lake Constance. Population-specific  $DR_{50}$  models were fit to data in Stewart, Mäkinen, et al. (2021) for *C. artedi* from lakes Superior and Ontario and *C. albula* from Lake S. Konnevesi. Species-specific  $DR_{50}$  models were taken from Eckmann (1987) for *C. lavaretus* (pelagic and littoral) from Lake Constance.

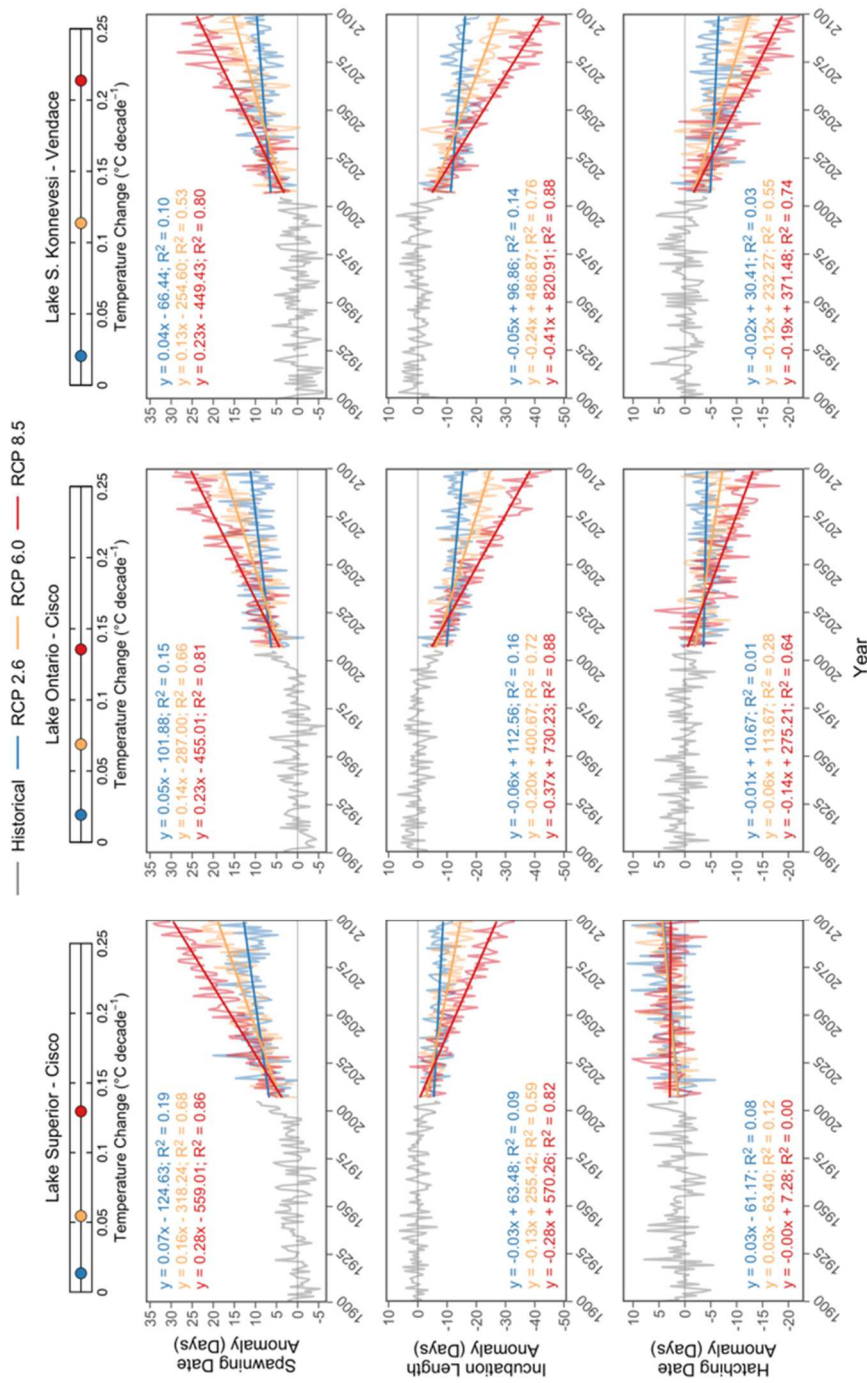


Figure 5.3: Simulation model anomalies (number of days) for spawning date, incubation length, and hatching date for cisco (*Coregonus artedii*) from lakes Superior and Ontario and vendace (*C. albus*) from Lake Southern Konnevesi. Anomalies were calculated for three representative concentration pathways (RCP) from 2007-2099 compared to the mean value from the historical period (1900-2006). The rate of simulated incubation temperature ( $^{\circ}\text{C}$ ) change per decade is indicated in the top row for each study group and matched to the respective RCP by color. Linear regression equations for each RCP scenario and the coefficient of determination ( $R^2$ ) was provided

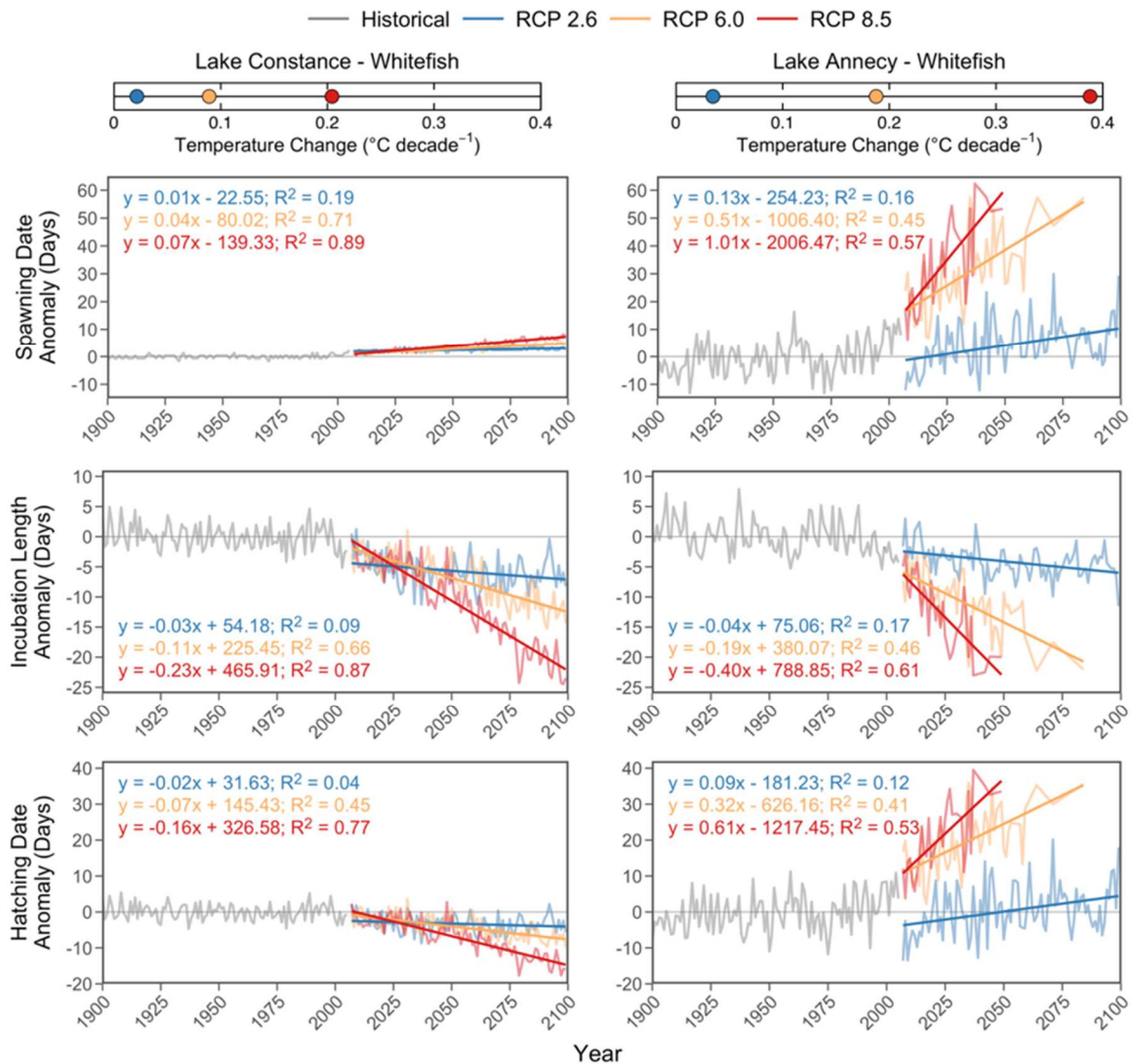


Figure 5.4: Simulation model anomalies (number of days) for spawning date, incubation length, and hatching date for European whitefish (*Coregonus lavaretus*) from lakes Constance and Annecy. Anomalies were calculated for three representative concentration pathways (RCP) from 2007-2099 compared to the mean value from the historical period (1900-2006). The rate of simulated incubation temperature (°C) change per decade is indicated in the top row for each study group and matched to the respective RCP by color. Linear regression equations for each RCP scenario and the coefficient of determination ( $R^2$ ) was provided.

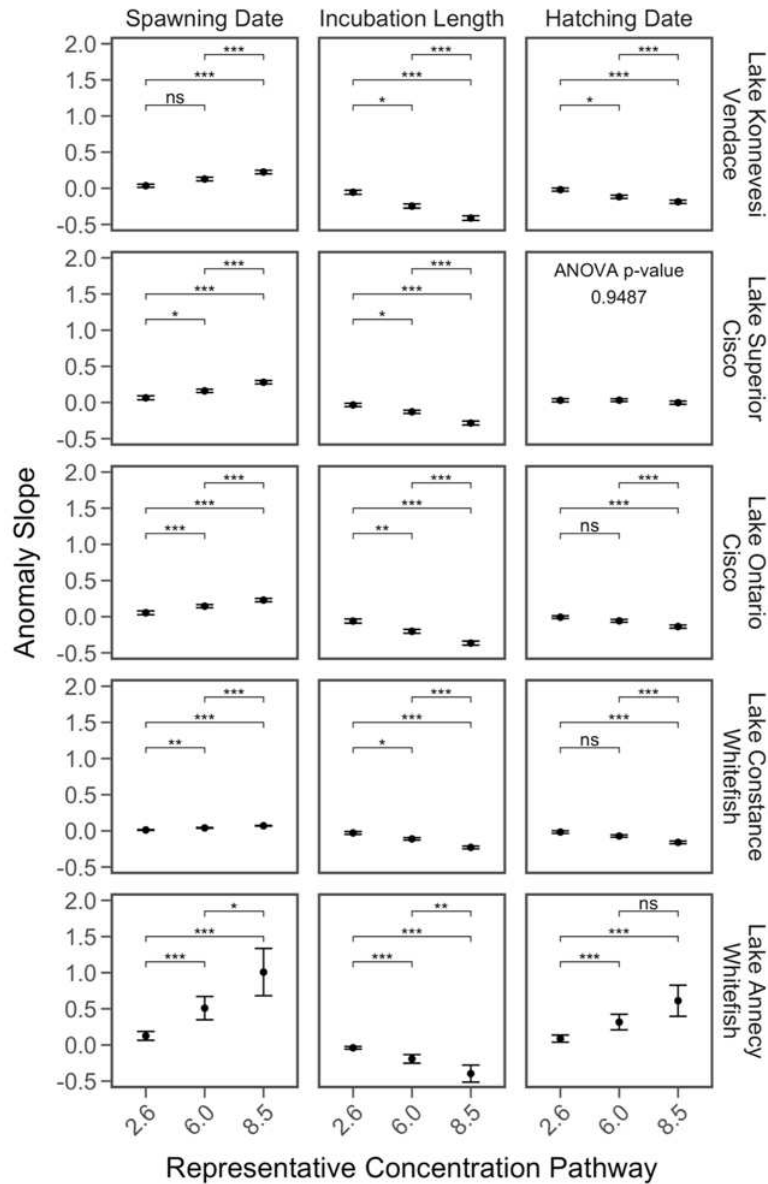


Figure 5.5: Anomaly slopes for spawning date, incubation length, and hatching date among representative concentration pathway (RCP) scenarios. Study groups included vendace (*Coregonus albula*), cisco (*C. artedi*) from lakes Superior and Ontario, European whitefish (*C. lavaretus*) from lakes Constance and Annecy). The p-value from Tukey post-hoc pairwise comparisons within each study groups is provided if the RCP p-value from the two-way ANOVA main effect was significant. Error bars indicate 95% confidence interval. \*\*\* < 0.001; \*\* < 0.01; \* = < 0.05; ns = Not Significant (> 0.05)

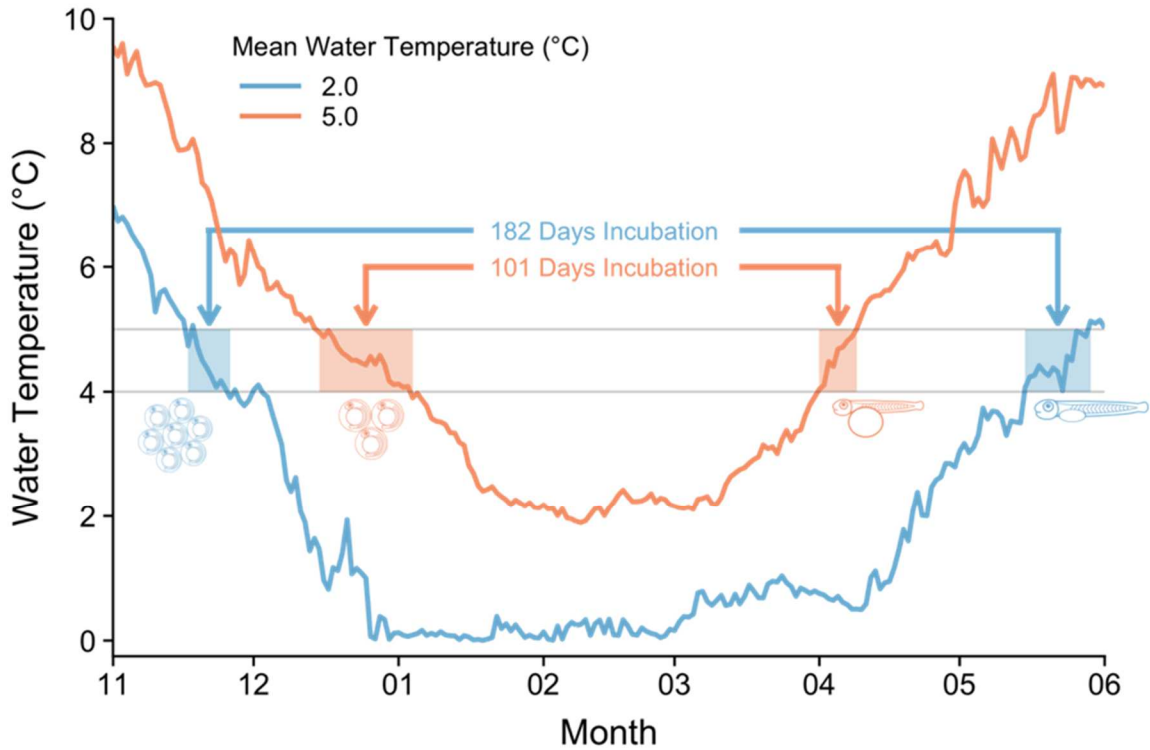


Figure 5.6: Theoretical winter incubation periods and responses of embryo demographics under normal (2.0°C; blue) and hypothetical warm (5.0°C; orange) winter thermal regimes. The shaded regions indicate spawning periods (left) and hatching periods (right) that may occur between 4-5°C. The 2.0°C temperature regime is water temperature data collected from Lake Superior at 10-m depth in 2018.

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APPENDIX A

Table A.1: Phenotypic variance component analysis for embryo survival (%) from Lake Southern Konnevesi vendace [LK-Vendace (*Coregonus albula*)], Lake Superior cisco [LS-Cisco (*C. artedii*)], and Lake Ontario cisco (LO-Cisco) across each incubation temperature treatment (°C).

Study Group	T°C	Female		Male		Female:Male		Error				
		$\sigma^2$	P	$\sigma^2$	P	$\sigma^2$	P	$\sigma^2$	%			
LK-Vendace	2.2	1.19	<0.001	24.53	0.12	0.481	2.53	0.24	0.211	4.92	3.29	68.03
	4.0	0.68	0.004	16.41	<0.01	0.999	<0.01	0.16	0.064	3.97	3.29	79.62
	6.9	0.89	<0.001	20.25	0.20	0.159	4.57	0.03	0.799	0.70	3.29	74.48
	8.0	0.33	0.007	8.33	0.20	0.074	4.97	0.14	0.078	3.49	3.29	83.21
LS-Cisco	2.0	1.61	<0.001	29.82	0.0	1.0	0.0	0.50	<0.001	9.25	3.29	60.94
	4.4	2.82	0.007	36.45	0.0	1.0	0.0	1.62	<0.001	20.97	3.29	42.58
	6.9	1.51	0.094	20.32	0.0	1.0	0.0	2.64	<0.001	35.44	3.29	44.24
	8.9	0.44	0.082	9.66	<0.01	0.999	<0.01	0.78	<0.001	17.29	3.29	73.04
LO-Cisco	2.0	0.55	0.450	11.28	0.0	1.0	0.0	1.01	0.295	20.90	3.29	67.82
	4.4	1.59	0.007	32.55	<0.01	0.999	<0.01	0.0	1.0	<0.01	3.29	67.45
	6.9	0.87	0.003	19.30	0.0	1.0	0.0	0.34	0.057	7.65	3.29	73.06
	8.9	0.71	<0.001	16.48	0.22	0.008	5.12	0.10	<0.001	2.24	3.29	76.17

Table A.2: Phenotypic variance component analysis for incubation period (number of days post-fertilization) from Lake Southern Konnevesi vendace [LK-Vendace (*Coregonus albula*)], Lake Superior cisco [LS-Cisco (*C. artedii*)], and Lake Ontario cisco (LO-Cisco) across each incubation temperature treatment (°C).

Study Group	T°C	Female			Male			Female:Male			Error	
		$\sigma^2$	P	%	$\sigma^2$	P	%	$\sigma^2$	P	%	$\sigma^2$	%
LK-Vendace	2.2	8.95	<0.001	21.27	0.87	0.160	2.08	0.0	1.0	0.0	32.25	76.65
	4.0	149.67	<0.001	30.03	26.12	0.023	5.24	9.79	0.138	1.96	312.80	62.76
	6.9	49.61	<0.001	18.93	0.92	0.815	0.35	10.18	0.008	3.89	201.37	76.84
	8.0	62.35	<0.001	42.32	1.02	0.693	0.69	7.26	0.001	4.93	76.69	52.06
LS-Cisco	2.0	233.62	<0.001	34.48	0.0	1.0	0.0	111.34	<0.001	16.43	332.54	49.08
	4.4	30.81	<0.001	27.53	5.82	0.115	5.20	7.32	<0.001	6.54	67.95	60.72
	6.9	7.04	0.001	18.37	1.83	0.089	4.76	1.51	0.024	3.95	27.95	72.92
	8.9	1.03	0.615	3.80	0.65	0.782	2.42	9.01	<0.001	33.34	16.34	60.44
LO-Cisco	2.0	123.54	<0.001	61.37	15.66	<0.001	7.78	1.70	0.002	0.84	60.41	30.01
	4.4	67.65	<0.001	48.78	16.22	<0.001	11.70	1.60	0.002	1.16	53.20	38.37
	6.9	25.00	<0.001	48.27	3.19	<0.001	6.16	0.34	0.086	0.66	23.25	44.91
	8.9	7.77	<0.001	29.95	0.80	0.012	3.10	0.44	0.032	1.70	16.93	65.26

Table A.3: Phenotypic variance component analysis for incubation length (accumulated degree-days) from Lake Southern Konnevesi vendace [LK-Vendace (*Coregonus albula*)], Lake Superior cisco [LS-Cisco (*C. artedii*)], and Lake Ontario cisco (LO-Cisco) across each incubation temperature treatment (°C).

Study Group	T°C	Female			Male			Female:Male			Error		
		$\sigma^2$	<i>P</i>	%	$\sigma^2$	<i>P</i>	%	$\sigma^2$	<i>P</i>	%	$\sigma^2$	<i>P</i>	%
LK-Vendace	2.2	187.78	<0.001	24.59	29.01	0.024	3.80	0.0	1.0	0.0	546.95	71.62	
	4.0	3,250.95	<0.001	30.56	549.52	0.025	5.17	210.28	0.142	1.98	6,625.67	62.29	
	6.9	2,622.69	<0.001	18.98	49.01	0.813	0.35	538.27	0.007	3.89	10,610.13	76.77	
	8.0	3,978.98	<0.001	41.44	36.31	0.825	0.38	489.35	0.001	5.10	5,097.39	53.09	
LS-Cisco	2.0	793.55	<0.001	33.84	0.42	0.997	0.02	399.38	<0.001	17.03	1,151.61	49.11	
	4.4	572.77	<0.001	27.51	108.43	0.115	5.21	136.38	<0.001	6.55	1,264.28	60.73	
	6.9	327.96	<0.001	18.34	85.05	0.090	4.76	70.59	0.024	3.95	1,304.32	72.95	
	8.9	80.39	0.600	3.84	51.62	0.777	2.47	693.60	<0.001	33.15	1,267.02	60.55	
LO-Cisco	2.0	388.91	<0.001	59.03	54.46	<0.001	8.27	5.74	0.003	0.87	209.73	31.83	
	4.4	1,258.57	<0.001	48.60	303.66	<0.001	11.73	30.77	0.001	1.19	993.64	38.49	
	6.9	1,167.10	<0.001	48.34	148.69	<0.001	6.16	15.58	0.090	0.65	1,082.77	44.85	
	8.9	599.46	<0.001	29.96	62.09	0.012	3.10	34.07	0.031	1.70	1,305.37	65.24	

Table A.4: Phenotypic variance component analysis for length-at-hatch (mm) from Lake Southern Konnevesi vendace [LK-Vendace (*Coregonus albula*)], Lake Superior cisco [LS-Cisco (*C. artedii*)], and Lake Ontario cisco (LO-Cisco) across each incubation temperature treatment (°C).

Study Group	T°C	Female			Male			Female:Male			Error	
		$\sigma^2$	<i>P</i>	%	$\sigma^2$	<i>P</i>	%	$\sigma^2$	<i>P</i>	%	$\sigma^2$	%
LK-Vendace	2.2	0.06	<0.001	37.01	0.02	0.011	11.06	0.0	1.0	0.0	0.08	51.93
	4.0	0.07	<0.001	41.39	0.02	0.007	9.74	0.0	1.0	0.0	0.09	48.87
	6.9	0.08	<0.001	49.84	0.0	1.0	0.0	0.01	0.227	3.82	0.08	46.34
	8.0	0.05	<0.001	34.13	0.01	0.239	6.14	0.02	0.033	9.92	0.08	49.81
LS-Cisco	2.0	0.49	<0.001	61.71	0.01	0.490	1.55	0.01	0.783	0.86	0.28	35.87
	4.4	0.20	<0.001	30.63	<0.01	0.999	<0.01	<0.01	0.910	0.56	0.44	68.81
	6.9	0.18	0.006	31.62	0.0	1.0	0.0	0.11	0.007	18.89	0.28	49.48
	8.9	0.10	0.001	29.00	0.01	0.465	3.17	0.0	1.0	0.0	0.23	67.83
LO-Cisco	2.0	0.12	<0.001	29.51	<0.01	0.908	0.23	0.0	1.0	0.0	0.28	70.26
	4.4	0.07	<0.001	13.63	<0.01	0.999	<0.01	0.0	1.0	0.0	0.42	86.37
	6.9	0.04	0.001	16.36	0.01	0.208	4.66	0.84	0.840	1.02	0.19	77.96
	8.9	0.02	0.078	8.95	0.0	1.0	0.0	0.05	0.050	12.60	0.21	78.44

Table A.5: Phenotypic variance component analysis for yolk-sac volume ( $\text{mm}^3$ ) from Lake Southern Konnevesi vendace [LK-Vendace (*Coregonus albula*)], Lake Superior cisco [LS-Cisco (*C. artedii*)], and Lake Ontario cisco (LO-Cisco) across each incubation temperature treatment ( $^{\circ}\text{C}$ ).

Study Group	T $^{\circ}\text{C}$	Female			Male			Female:Male			Error	
		$\sigma^2$	P	%	$\sigma^2$	P	%	$\sigma^2$	P	%	$\sigma^2$	%
LK-Vendace	2.2	<0.01	0.007	14.06	0.0	1.0	0.0	<0.01	0.830	1.12	<0.01	84.82
	4.0	<0.01	0.005	20.51	<0.01	0.179	6.71	<0.01	0.373	4.69	<0.01	66.38
	6.9	<0.01	0.007	28.09	<0.01	0.991	0.07	<0.01	<0.001	23.51	<0.01	43.19
	8.0	<0.01	<0.001	32.74	<0.01	0.697	1.39	<0.01	0.008	9.53	<0.01	35.93
LS-Cisco	2.0	0.02	0.030	25.48	0.0	1.0	0.0	0.01	0.001	20.11	0.04	54.42
	4.4	0.01	0.008	33.64	<0.01	0.784	1.78	0.01	0.050	13.49	0.02	51.10
	6.9	<0.01	0.151	14.07	<0.01	0.846	1.81	0.01	0.058	17.15	0.04	66.98
	8.9	0.02	0.230	8.87	0.01	0.487	4.93	0.02	0.192	10.90	0.13	75.31
LO-Cisco	2.0	0.02	<0.001	39.32	<0.01	0.816	0.39	0.0	1.0	0.0	0.03	57.63
	4.4	0.02	<0.001	56.43	<0.01	0.468	1.57	0.01	0.293	2.89	0.01	39.11
	6.9	0.04	<0.001	41.84	<0.01	0.999	<0.01	<0.01	0.096	5.55	0.05	52.61
	8.9	0.05	<0.001	32.90	<0.01	0.699	0.80	0.0	1.0	0.0	0.10	66.30

## APPENDIX B

Table B.1: Years of *in situ* data used for model validation.

Study Group	Water Temperature	Spawning	Hatching
Lake Superior (Apostle Islands)	2016-18	2016-18	2016-18
Lake Superior (Thunder Bay)	2017-21	2005; 2007-08; 2010	2008-09
Lake Ontario	2012-21	2007; 2017; 2019-20	2004-06
Lake S. Konnevesi	2019-21	2019-21	2019-21
Lake Geneva	2010-2021	2016-19	2016
Lake Annecy	2005-06	2017-18; 2021	2004-07

Table B.2: Study group and modeled case-study lakes from Inter-Sectoral Impact Model Intercomparison Project that match study group parameters (the lakes that were averaged together by category).

Lake Type	Lake Name	Latitude	Longitude	Climate Zone	Depth Bin (m)
Study Group	Geneva	46.37	6.45	Northern Temperate	0-10
	Annecey	45.86	6.17	Northern Temperate	0-10
	Ontario	44.05	-76.20	Northern Temperate	0-10
	Superior (Thunder Bay)	48.41	-89.02	Northern Temperate	10-25
	Superior (Apostle Islands)	46.85	-90.55	Northern Temperate	10-25
	Southern Konnevesi	62.58	26.58	Northern Cool	0-10
Modeled Case Study	Mueggelsee	52.43	13.65	Northern Temperate	0-10
	Allequash	46.04	-89.62	Northern Temperate	0-10
	Trout Bog	46.04	-89.69	Northern Temperate	0-10
	Crystal Bog	46.01	-89.61	Northern Temperate	0-10
	Wingra	43.05	-89.43	Northern Temperate	0-10
	Esthwaite-Water	54.37	-2.99	Northern Temperate	10-25
	Big Muskellunge	46.02	-89.61	Northern Temperate	10-25
	Sparkling	46.01	-89.7	Northern Temperate	10-25
	Crystal Lake	46.00	-89.61	Northern Temperate	10-25
	Two-Sisters	45.77	-89.53	Northern Temperate	10-25
	Dickie	45.15	-79.09	Northern Temperate	10-25
	Great	44.53	-69.89	Northern Temperate	10-25

Fish	43.29	-89.65	Northern Temperate	10-25
Mendota	43.10	-89.41	Northern Temperate	10-25
Delavan	42.61	-88.6	Northern Temperate	10-25
Kuivajarvi	60.47	23.51	Northern Cool	0-10
Vortsjaerv	58.31	26.01	Northern Cool	0-10
Nohipalo- Mustjaerv	57.93	27.34	Northern Cool	0-10
Laramie	40.62	-105.84	Northern Cool	0-10

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Table B.3: Linear regression equations fit to embryo survival (%) between two temperature treatments for cisco (*Coregonus artedii*) from lakes Superior and Ontario, vendace (*C. albula*) from Lake Southern Konnevesi, and European whitefish (*C. lavaretus*) from Lake Constance. Embryo survival at temperature data were taken from Stewart, Mäkinen, et al. (2021) and unpublished data (EL and CG).

Study Group	Species	Source	Temperature Range (°C)	Survival Regression
Lake Superior	<i>C. artedii</i>	Stewart et al., 2021	2.0 - 4.4	$y = 0.8418 - 0.0208x$
			4.4 - 6.9	$y = 0.7165 + 0.0077x$
			6.9 - 8.9	$y = 0.8945 - 0.0181x$
Lake Ontario	<i>C. artedii</i>	Stewart et al., 2021	2.0 - 4.4	$y = 0.9945 - 0.0007x$
			4.4 - 6.9	$y = 1.0623 - 0.0160x$
			6.9 - 8.9	$y = 1.7403 - 0.1143x$
Lake S. Konnevesi	<i>C. albula</i>	Stewart et al., 2021	2.2 - 4.0	$y = 0.9346 - 0.0446x$
			4.0 - 6.9	$y = 0.6743 - 0.0205x$
			6.9 - 8.0	$y = 1.6420 - 0.1197x$
Lake Constance	<i>C. lavaretus</i> (pelagic)	unpublished data, EL and CG	7.0 - 9.0	$y = 2.4507 - 0.2150x$
Lake Constance	<i>C. lavaretus</i> (littoral)	unpublished data, EL and CG	7.0 - 9.0	$y = 3.0107 - 0.2900x$