Influence of changing lake temperatures on coregonine embryogenesis at local to global scales

Taylor R. Stewart1,5, Mikko Makinen2, Chloé Goulon3, Jean Guillard3, Timo Marjomäki2, Emilien Lasne4, Juha Karjalainen2, and Jason D. Stockwell5

1Department of Biology, University of Vermont, USA

2University of Jyväskylä, Finland

3UMR CARRTEL INRAE-Université Savoie Mont Blanc, France

4UMR ESE Agrocampus Ouest-INRAE, France

5Rubenstein Ecosystem Science Laboratory, University of Vermont, USA

**ABSTRACT:**

Will write after feedback.

**INTRODUCTION:**

Aquatic ecosystems are rich in biodiversity, provide a diverse array to habitats, and produce numerous socio-economic benefits (Halpern et al. 2015, Langhans et al. 2019). Many of these valuable ecosystems have experienced detrimental impacts from human stressors and are being further impacted from climate change (Vörösmarty et al. 2010, Langhans et al. 2019). These pressures create unique and difficult challenges for biodiversity conservation and ecosystem sustainability. To counteract these challenges, a foundational understanding of the primary threats to aquatic ecosystems and organisms at a range of spatial scales from local to global is needed (Vörösmarty et al. 2010, Halpern et al. 2015, Langhans et al. 2019).

Freshwater lakes are one of the most sensitive ecosystems to climate change (Woolway et al. 2020). Climate change can alter lake physical and chemical characteristics that result in both direct and indirect biological consequences for lake ecology (Adrian et al. 2009, Williamson et al. 2014). One of the greatest threats to lakes from climate change are rising water temperatures, which are occurring at an unprecedented rate on a global scale (Austin and Colman 2007, O’Reilly et al. 2015, Woolway et al. 2017). Conversely, water temperature change is not projected to rise at a consistent rate across regions, seasons, or lake types (O’Reilly et al. 2015, McCullough et al. 2019). 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), and the greatest seasonal increase in air temperature is expected during winter in northern Europe and North America (Christensen et al. 2007). Changes in spring conditions and increases in the length of the frost-free season can prolong annual growing seasons with warmer summers, longer autumns, shorter ice-cover duration, and rapid spring water warming (Meehl et al. 2007). Although the broader impacts of climate-derived changes in lake dynamics remain unclear (Shatwell et al. 2019), the responses of many lake organisms are projected to be inadequate to counter the speed and magnitude of climate change, leaving some species vulnerable to decline and extinction (Hoffmann and Sgrò 2011).

Temperature is considered an abiotic master factor for aquatic ecosystems, as changes in water temperature directly alter the physical and chemical properties of water and affect phenological and reproductive events, metabolic rates, growth, and survival of aquatic organisms (Brett 1979, Little et al. 2020). 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 ranges, live near their thermal limits, or develop over long periods at cold temperatures are at-risk under warming climate scenarios as temperature can have strong effects at early-life stages (Blaxter 1991, Pepin 1991, Ficke et al. 2007, Lim et al. 2017). Unlike their marine counterparts, most freshwater fishes are restricted to lake systems which impedes their capability to evade the effects of climate change due to the isolated nature of lakes (Ficke et al. 2007). ﻿Shifts in physiology of lake fish populations living close to their physiological limits (*e.g.,* coregonines in the Laurentian Great Lakes) will be required if species are to persist under increasingly stressful thermal conditions (Woolsey et al. 2015, Howells et al. 2016). Fundamental questions for evolutionary and conservation biologists in a global change context include how lake fishes will respond to rising water temperatures and what mechanisms will be involved in the process.

Freshwater whitefishes, Salmonidae Coregoninae (hereafter coregonines), are of great socio-economic value (Nyberg et al. 2001, Ebener et al. 2008a, 2008b, Vonlanthen et al. 2009, 2012, Lynch et al. 2015, 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 and Bell 2011, Jeppesen et al. 2012, Isaak 2014, Jonsson and Jonsson 2014, Karjalainen et al. 2015, 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). The reasons for declining recruitment are unknown, but winter conditions appear to play a role in recruitment success (Nyberg et al. 2001, Marjomäki et al. 2004, Karjalainen et al. 2015, 2016). Coregonines generally spawn during late-fall, embryos incubate over winter, and begin hatching in late spring (Karjalainen et al. 2000, Stockwell et al. 2009). This long period of reproduction and embryo development leaves coregonines exposed to a variety of thermal conditions and seasonal thermal regimes are changing (Karjalainen et al. 2015, Winslow et al. 2017). At least some coregonines, however, have the ability to adapt to temperature changes within the limits of phenotypic plasticity and through genetic adaptive changes (Karjalainen et al. 2015, 2016).

Geographic variation is important to consider alongside the limits of phenotypic plasticity. Fish populations can show differential long-term adaptation to climates across a latitudinal gradient (Conover and Present 1990, Yamahira and Conover 2002, Chavarie et al. 2010, Wilder et al. 2020). As ectotherms, fishes at high-latitudes experience low temperatures overall and shorter growing seasons and should exhibit lower standard metabolic rates, growth rates, and smaller size-at-age than individuals at lower latitudes (Reist et al. 2006). However, for cold-water stenothermic fishes, the water temperatures throughout the water column at lower latitudes may exceed their optimal range for significant portions of the growing season, while water temperatures at higher latitudes may remain near the optimum for maximal growth efficiency throughout the growing season (Conover and Schultz 1995). As water temperature is an abiotic master factor for fish physiology and can vary across a latitudinal gradient, there is a wide range of future possibilities in how populations may respond to increasing temperatures across latitudes (Reist et al. 2006). Coregonines occur broadly across northern latitudes and are an ideal group to identify how cold-water fishes may adapt to climate-driven shifts in environmental variables, such as water temperature. Large-scale experimental studies may aid in understanding the adaptive thermal capacity of fishes from different latitudes and what level of adaptive response is needed to mitigate the effects of changing local environments (Hoffmann and Sgrò 2011).

Our objective was to experimentally analyze the reaction norms of early-life stage coregonines, from known breeding crosses, from across a broad latitudinal gradient to changing winter incubation temperatures. We hypothesized that coregonine populations across latitudes would have differential levels of phenotypic plasticity in life-history traits of embryos and morphological traits of larvae in response to warming winter conditions. We used the following framework to contrast the thermal response found among populations: high-latitude populations which experience lower water temperatures and longer winters, compared to lower-latitude populations, are expected to (1) have prolonged incubation periods across all temperatures, (2) have lower embryo survival as temperature increases, and (3) exhibit a smaller size-at-age across all temperatures. We also hypothesized that coregonine adults would have a parental effect on the short-term resilience of offspring to changing winter conditions. We expect a higher parental response at warmer temperatures that induce a higher thermal stress response. We also expect that early-life stage traits will have different levels of heritability and maternal effects based on the developmental stage; with traits more closely associated with egg size having a greater maternal effect and being less heritable.

**METHODS:**

Study Sites and Collections

We used a cross-lake, cross-continent, cross-species approach to evaluate the responses and thermal tolerances of coregonine embryos and larvae to changing thermal regimes. Wild-caught populations of cisco (*C. artedi*) in Lake Superior (LS-Cisco; USA/Canada) and Lake Ontario (LO-Cisco; USA/Canada), and vendace (*C. albula*; LK-Vendace) and European whitefish (*Coregonus lavaretus*; LK-Whitefish) in Lake Konnevesi (Finland; Figure 1) were sampled using live-capture gear. Adult field collections occurred during coregonine spawning periods for Lake Ontario and Lake Superior. On Lake Konnevesi, adults were collected prior to spawning and stored in an aquaculture pool with water fed directly from the lake until spawning was initiated. A single laboratory in North America (University of Vermont (UVM), USA) and Europe (University of Jyväskylä (JYU), Finland) conducted all sampling, fertilization, and experimental work for populations on each continent.

The term population is used in many ways. For the sake of clarity, our operational use of a population is to represent a single species within a single lake (*e.g.,* cisco in Lake Superior).

Fertilization and Incubation

Eggs and milt were stripped from dams and sires from each population and artificially fertilized under a blocked, nested full-sib, half-sib fertilization design (Figure 2) to create a maximum of 48 full-sibling families nested within half-siblings per population. This fertilization design was used to maximize the amount of genetic variation and minimized the potential loss of multiple families if a dam or sire produced poor quality gametes, compared to a full-factorial design. Pairing was performed by dividing the adults used in the experiment into three or four fertilization blocks. A single block consisted of four sires each paired to three unrelated dams, where all offspring of a given dam were full siblings. Fertilizations were performed block by block to ensure germ cell survival.

Approximately 200 eggs per dam were fertilized by approximately 10 μl of milt from each sire 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 2-3 times until the water was clear. Water used during fertilizations was reconstructed freshwater (OECD ISO 6341:2012) to standardize the chemical properties of the water used among populations 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 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 Konnevesi. Demographic data (*e.g.,* total length and weight) were collected on adults.

Fertilization success was determined by haphazardly taking 10 embryos from each family and assessing under microscopy within 72-hours post-fertilization (Oberlercher and Wanzenböck 2016). If fertilization was low (<30%), the family was removed from the experimental setup. Embryos from successfully fertilized families were individually distributed into 24-well cell culture microplates and incubated in 2 ml of reconstructed freshwater. Reconstructed freshwater was used during incubation to maintain sterility, prevent bacterial growth in the wells, and eliminate the need for harsh fungicide treatments on the embryos. A total of 36 embryos per family were used for Lake Konnevesi and 48 embryos per family for Lake Ontario and Lake Superior. 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 species and population were incubated at constant temperatures of 2.0, 4.5, 7.0, and 9.0°C and randomly placed in climate-controlled chambers at UVM (Memmert® IPP260Plus) and climate-controlled rooms at JYU (Brand). 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 prevent excessive evaporation. Microplate orientation and position were rotated weekly to eliminate any temperature heterogeneity within the chambers and rooms. Water temperatures were recorded hourly with loggers (HOBO® Water Temperature Pro v2 at UVM and Escort iMini at JYU) and daily mean water temperatures calculated. Incubations took place in the dark, with the exception of short 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. All newly hatched larvae were photographed for life-history and morphological traits.

Statistical Analyses

*Life-history and Morphological Traits*

Embryo survival was estimated as the percent of embryos surviving between the eye-up and hatch stages. Incubation period was assessed by two variables: the number of days from fertilization to hatching (days post-fertilization) and the sum of the degree-days (accumulated degree-days). Total length-at-hatch (mm) and yolk-sac volume (YSV; mm3) 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 1963):

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

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 induced from fertilization failure produced inequalities in the number of offspring among families and an unbalanced design. The sample size for incubation period is a function of embryo survival and subsequently resulted in an unbalanced design. Therefore, binary data (*i.e.,* embryo survival) were analyzed with binomial generalized linear mixed-effects models (LMM) and normally distributed data (*i.e.,* incubation period, length-at-hatch, and yolk-sac volume) were analyzed with restricted maximum likelihood LMMs with the lme4 package (Bates et al. 2015). Population and incubation temperature were included as fixed effects and sire, dam, family (sire and dam combination), and fertilization block as random effects. Because embryos were raised independently, the replication unit in the statistical models is the individual embryo. All traits were examined for population and incubation temperature effects in addition to individual parental effects (dam and/or sire effects), fertilization block, and all possible interactions with backward, stepwise effect-selection using the buildmer package (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. The mixed-effects model output does not produce significance values for model effects; therefore, significance for population, 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. Post-hoc pairwise comparisons on significant fixed effects were performed with the emmeans package (Lenth 2020). Each species was fit independently to eliminate any confounding effects between continents and among species resulting in three models: Lake Superior and Lake Ontario cisco, Lake Konnevesi vendace, and Lake Konnevesi European whitefish.

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*Parental Response*

In addition to population-level effects, life-history and morphological traits were analyzed for heritability, or the proportion of additive genetic phenotypic variance, and maternal effect, or the non-genetic contribution from the mother’s phenotype. The variance components and heritability estimates were assessed using non-parametric bootstrapping to address unbalanced family sizes. ﻿We generated a bootstrap sample by resampling, with replacement, the individuals within each family, population, and incubation temperature treatment until the number of observations in the original sample was reproduced for each of the traits. Individuals were resampled to account for within-family variation and ensure that the genetic effects were not overestimated (Neff and Fraser 2010). From the resampled data, the phenotypic variance was partitioned into random effects for sire (VS), dam (VD), sire:dam (VS:D), and random residual (VE) variance components using mixed-effects models with the fullfact package (Houde and Pitcher 2019) for each population and incubation temperature treatment. The resampling and variance calculations were repeated 10,000 times.

Under our fertilization design, the variance among half-sib families (VS) represents one-fourth of the additive genetic variance (VA) and can therefore be used to estimate VA and the narrow-sense heritability (h2; hereafter heritability), assuming that epistasis is negligible (Lynch and Walsh 1998). Additive genetic variance was calculated as four times the sire component of variation and maternal variance (VM) as dam variance minus sire variance: ; . Total phenotypic variance (VP) was portioned into additive genetic variance, maternal variance, and random residual variance: . Heritability was calculated as the ratio of additive genetic to total phenotypic variance for each population and incubation temperature treatment: . Similarly, to heritability, the non-genetic maternal effect was calculated as . Heritabilities and maternal effects were estimated for each bootstrap resample and the bias-corrected median and standard error was determined from the empirical bootstrapped distributions. Both estimates are presented as proportions. European whitefish from Lake Konnevesi was removed from this analysis due to a low number of families.

All analyses were performed in R version 4.0.3 (R Core Team 2020).

**RESULTS:**

Incubation Water Temperatures

Water temperature during incubations were maintained near the target incubation temperature for 2.0°C and 7.0°C for both labs. Incubation water temperature at 4.5°C and 9.0°C were lower than the target incubation temperature at JYU, but not at UVM (Table 1).

Spawning Adults

Total lengths and fresh mass of spawning adults used for gamete collection varied widely among populations (Table 2). LK-Vendace were notably smaller than all other populations. The remaining populations varied less in size, but LK-Whitefish were smaller than LS-Cisco and LO-Cisco. The size of spawning adults was negatively related to latitude and differed among species (Table 2).

The LK-Vendace females had smaller egg diameters (mean (SD) = 1.58 mm (0.11)) than the two cisco populations (LS-Cisco: mean (SD) = 2.14 (0.12); LO-Cisco: mean (SD) = 2.30 (0.08)). No egg diameter measurements were available for LK-Whitefish.

Life-history and Morphological Traits

All cisco traits, except length-at-hatch, had significant interaction effects between population and incubation temperature (maximum *P* < 0.001), and thus precluded any interpretation of main effects (Tables 3 and 4). All vendace and European whitefish temperature main effects were significant (maximum *P* < 0.001; Tables 3 and 4). Below we describe the interaction effects and temperature pairwise comparisons for each trait. All statistical model results can be found in Tables 3 and 4.

*Embryo Survival*

The effect of population depended on temperature because the ﻿differences in cisco embryo survival among populations were more pronounced at higher temperatures. All pairwise temperature comparisons for vendace and European whitefish were significant (maximum *P* = 0.005), except for 2.2-6.9°C for vendace (*P* = 0.665) and 4.0-6.9°C for European whitefish (*P* = 0.282). Embryo survival was highest among all populations at 2.0°C. LO-Cisco had the highest embryo survival up to 7.0°C and then decreased rapidly at 9.0°C. LS-Cisco and LK-Vendace embryo survival was less variable across all temperatures. Embryo survival in LK-Whitefish was lowest among populations and consistently decreased as temperature increased (Figure 3). The greatest decrease in embryo survival between the coldest and warmest treatments was in LO-Cisco, our southernmost population (Figure 3). However, all populations, except LK-Whitefish, saw arguably high embryo survival across all temperature treatments.

*Incubation Period (days post-fertilization)*

The effect of population depended on temperature because the differences in the number of days post-fertilization among populations was more pronounced at colder temperatures. All pairwise temperature comparisons for vendace and European whitefish were significant (maximum *P* < 0.001). The number of days post-fertilization was highest for all populations at 2.0°C and decreased as temperature increased. Higher-latitude populations (*i.e.,* LK-Vendace and LK-Whitefish) had longer incubation periods compared to lower-latitude populations (*i.e.,* LS-Cisco and LO-Cisco) across all temperatures (Figure 3).

*Incubation Period (accumulated degree-days)*

The effect of population depended on temperature because the differences in accumulated degree-days among populations was more pronounced at higher temperatures. All pairwise temperature comparisons for vendace and European whitefish were significant (maximum *P* = 0.002). Accumulated degree-days were highest for all populations at 7.0°C and decreased at all other temperatures. Higher-latitude populations (*i.e.,* LK-Vendace and LK-Whitefish) had larger differences in accumulated degree-days across temperature compared to lower-latitude populations (*i.e.,* LS-Cisco and LO-Cisco). In particular, LK-Vendace had the longest incubation periods, even when exposed to warm temperatures (*i.e.,* high accumulated degree-days; Figure 3).

*Length-at-Hatch*

Length-at-hatch had a uniform response to temperature among populations across the latitudinal gradient as all populations decreased in length-at-hatch as temperature increased. All pairwise temperature comparisons for vendace were significant (maximum *P* < 0.001), except for 2.2-4.0°C (*P* = 0.998). Only European whitefish pairwise temperature comparisons with 8.0°C were significant (maximum *P* < 0.001). Temperature and population main effects were significant for cisco. All pairwise population and temperature comparisons for cisco were significant (maximum *P* < 0.001; Table 4). All populations showed a decrease in length-at-hatch as temperature increased. LO-Cisco had the largest length-at-hatch across all temperatures. LK-Vendace had a large difference in length-at-hatch and were significantly smaller compared to all other populations (Figure 4). Both vendace and European whitefish had approximately the same length-at-hatch from 2.0-7.0°C with a sharp decrease at 8.0°C. In contrast, both cisco populations had a constant decline in length-at-hatch from 2.0-9.0°C (Figure 4).

*Yolk-sac Volume*

All pairwise temperature comparisons for vendace and European whitefish were significant (maximum *P* < 0.001), except for 2.2-4.0°C for European whitefish (*P* = 0.059). Yolk-sac volume was highest for all populations at 9.0°C and decreased as temperature decreased. LK-Vendace had a large difference in yolk-sac volume and was significantly smaller compared to all other populations. Excluding LK-Vendace, yolk-sac volume dropped more rapidly as temperature decreased at higher-latitude populations (*i.e.,* LK-Whitefish) compared to lower-latitude populations (*i.e.,* LS-Cisco and LO-Cisco). Yolk-sac volume between cisco populations decreased as temperature increased, but the difference in yolk-sac volume increased between cisco populations as temperature decreased (Figure 4). Yolk-sac volume in LK-Whitefish had a similar trend but to a greater magnitude than found in cisco populations (Figure 4).

The difference in the size of spawning LK-Vendace adults and smaller eggs eliminated our ability to compare LK-Vendace length-at-hatch and yolk-sac volume results to all other populations.

Parental Response

The dam effect was significant in all life-history and morphological traits for all species (Tables 3 and 4). The sire effect was significant for days post-fertilization and accumulated degree-days in cisco and vendace, length-at-hatch in vendace, and embryo survival and yolk-sac volume in European whitefish (Tables 3 and 4). Heritability estimates in life history and morphological traits in response to temperature were < 0.40 (Tables 5 and 6). Embryo survival, length-at-hatch, and yolk-sac volume showed the lowest degree of heritability across all populations (Tables 5 and 6). Incubation period (both days post-fertilization and accumulated degree-days) had the highest heritability, with LO-Cisco and LK-Vendace having the highest heritability estimates at colder temperatures and LS-Cisco at the warmer temperatures (Table 5). Length-at-hatch heritabilities were variable (Table 6). The relative importance of the maternal variance was examined and explained a moderate portion of the phenotypic variance. Incubation period (both days post-fertilization and accumulated degree-days) showed opposing trends in the maternal effect between cisco and vendace populations. LK-Vendace incubation period (both days post-fertilization and accumulated degree-days) showed low maternal effects at cold temperatures and a rapid increase at 9.0°C, while cisco populations had high maternal effects at cold temperatures and decreased as temperature increased (Table 5). Cisco populations had higher maternal effects for all traits at colder temperatures with LO-Cisco always higher than LS-Cisco, except for embryo survival. Overall, we found low levels of heritability but higher levels of maternal effects for embryo survival, length-at-hatch, and yolk-sac volume; three traits highly correlated to egg size (Tables 5 and 6). However, incubation period (both days post-fertilization and accumulated degree-days) had moderate levels of both heritability and maternal effects (Table 5).

**DISCUSSION:**

Our incubation experiments demonstrated substantial latitudinal variation in reaction norms for both life-history and morphological traits of early-life coregonines in response to temperature. This provides evidence that coregonines do exhibit adaptation to latitude and possess a high level of thermal plasticity in some traits. First, we found a high degree of local adaptation towards long incubation periods within-populations at high-latitudes. Second, yolk-sac volume had a strong, positive relationship with temperature within- and among-populations across latitudes and was negatively correlated with length-at-hatch. Lastly, differential levels of parental effects were found within- and among-populations and traits.

We hypothesized that coregonine populations across latitudes differentially respond to changing winter conditions. All life-history and morphological traits examined, except embryo survival, showed some form of latitudinal gradient to incubation temperature and suggests that coregonines are thermally adaptable. The lack of variation in embryo survival among populations was surprising because temperature is known to be the main force determining coregonine embryo development and survival (Colby and Brooke 1970, Brooke and Colby 1980, Luczynski and Kirklewska 1984, Karjalainen et al. 2015). Although we did not see any latitudinal variation in embryo survival, Lake Ontario, our southernmost population, did have the strongest negative response to temperature suggesting that embryo survival in low-latitude populations may be the most vulnerable to rising temperatures. Most coregonines, like many freshwater fishes, do not have the opportunity to migrate to colder waters due to the isolated nature of lakes. This result suggests that shifts in the developmental physiology of populations living close to their thermal threshold would be required if coregonines are to persist under increasingly stressful conditions.

High-latitude populations typically have long incubation periods as winter and the ice-covered season is disproportionately longer than at lower latitudes. Winter typically has cold weather, decreased daylight, and limited biotic growth and increases in severity with latitude. Our result that incubation periods from high latitude populations were the longest incubation periods, even when exposed to high temperatures, suggests a high degree of local adaptation towards long incubation periods. Increases in spring water temperature cues the onset of hatching in autumn-spawning coregonines and hatching is typically synchronized with ice-out (Urpanen et al. 2005). However, if winter water temperatures during incubation rise, the ability to match optimal spring conditions may be weakened. Populations that are more resilient to increasing or variable winter incubation temperatures may have a better opportunity to regulate ontogeny and control the timing of hatching. This provides populations the ability to (1) ensure adequate embryo developmental time and mitigate premature hatching that can lead to high levels of larval deformities and mortality, and (2) match the spring plankton bloom to support exogenous larval feeding and buffer against starvation.

Spawning strategies of fish can be variable, occurring from daily to once in a lifetime or ranging across all seasons (McBride et al. 2015). For many fish species, spawning strategies and breeding patterns are constrained by the adult body condition and the environment. In this context, our result on embryo incubation periods from low-latitude populations not being prolonged when exposed to high temperatures was particularly interesting. High-latitude populations typically spawn earlier in autumn and may have the opportunity to shift timing of reproduction later into the season, while still providing an adequate incubation period for embryo development, if water temperatures continue to rise. However, low latitude populations already spawn in late-autumn and may not have time for embryos to fully develop if incubation periods are shortened from rising water temperatures and do not have the thermal plasticity to withstand high temperatures. This potentially opens the question: is there an adaptive opportunity for lower latitude populations to have a subsequent spawning event peak later in the winter if temperatures continue to rise? Winter spawning populations may leave the spawning adults and their offspring less vulnerable to contemporary climate change. However, this shift would present significant biological challenges and require a high and rapid evolutionary investment in the spawning adults to avoid complications in ovulation, egg quality, and embryo development. Poor-feeding or metabolically costly environments may not allow for adults to efficiently support gametogenesis, especially oogenesis in females (McBride et al. 2015).

Contrasting spawning strategies of genetically similar fish are known to happen within other fish species. Atlantic herring (*Clupea harengus*) have both autumn- and winter-spawning stocks in the North Sea. Both Atlantic herring spawning stocks share the same summer feeding grounds and start oocyte development at the same time, but have different fecundity and egg sizes (van Damme et al. 2009). Winter spawners continue oocyte development through autumn and result in a lower number of larger eggs compared to the autumn-spawning stock (van Damme et al. 2009). Oocyte development is driven by body energy content and winter-spawning stocks may give females the chance to mitigate the disproportionate energy demand toward gomatic growth during the summer when metabolic demands are higher. Alternatively, skipped spawning stocks may allow for iteroparous adults to avoid the high energetic cost of spawning if the adult condition is not adequate (Jørgensen et al. 2006, van Damme et al. 2009). Changes in the environment and the condition of an individual spawning adult could affect future coregonine spawning strategies. The occurrence of sympatric coregonine species that are distinguished by differential spawning times is common throughout northern-Eurasian lakes (Schulz and Freyhof 2003, Schulz et al. 2006). Autumn, winter, and spring-spawning coregonines are known to co-occur and the main taxonomic trait distinguishing these sympatric species is spawning time (Schulz and Freyhof 2003, Schulz et al. 2006, Ohlberger et al. 2008). Further work examining reproductive plasticity of coregonine adults is needed but our results suggest that embryos from low-latitude, autumn-spawning populations are not resilient to rising water temperatures during incubation. The adaptive response to warmer winter conditions would need to occur within adult life-history strategies.

Lake morphology is important to consider alongside the question of a winter- or spring-spawning adaptation as deeper lakes could provide colder thermal refuge at greater depths if suitable spawning habitat is available. Numerous studies have examined if future suitable thermal and oxythermal habitat for cisco will exist (Jacobson et al. 2010, Herb et al. 2014, Schmitt et al. 2020). Predictions show cold-water habitat in lakes to decrease under future climate scenarios and the remaining thermal habitat to decrease in quality (Herb et al. 2014). Models project deeper and less eutrophic lakes to provide the best cold-water habitat as water temperatures and land uses change. However, cisco populations appear to be more thermally tolerant than other cold-water species and have the potential to maintain thermal refugia in lakes (Jacobson et al. 2010, Herb et al. 2014, Schmitt et al. 2020). While deep lakes may possess acceptable thermal refugia for coregonines, access to suitable spawning and incubation habitat is unknown for most populations.

We also found different responses in morphological traits (*i.e.,* length-at-hatch and yolk-sac volume) among populations. Our results suggest that higher- and lower-latitude populations may have differential responses to temperature with low-latitude populations affected more than high-latitude populations. This differential response is likely confounded by the different responses found in incubation periods and directly influenced by the number of days post-fertilization and accumulated degree-days. However, yolk-sac volume had a stronger response to temperature among populations across latitudes compared to length-at-hatch. The trade-off between length-at-hatch and yolk-sac volume is well documented in larval fish physiology (Blaxter 1991). The challenge for managers making conservation decisions about temperature adaptation in coregonines is to determine what trait is most important. Length-at-hatch and yolk-sac volume are negatively correlated and both traits can have large implications on larval survival. Conserving yolk-sac during development extends endogenous feeding and delays starvation after hatching. Hatching at a larger size allows larvae to swim more effectively, be less vulnerable to predation, and feed more efficiently. Spring conditions, larval nursery habitat, and larval prey community structure all need to be considered when taking into account the relative importance of each morphological trait.

Climate change impacts may only exacerbate the importance of each morphological trait in determining either a match or mismatch between larval predators and their zooplanktonic prey. Using winter water temperatures collected from Lake Superior, we can show the theoretical interactions among water temperature, spawning period, incubation period, length-at-hatching, and yolk-sac volume supported by our results (Figure 5). If spawning does shift to a later period from rising water temperatures, we would expect the size of eggs to increase and the fecundity of females to decrease (Figure 5). 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 Konnevesi vendace and European whitefish have been shown to have high flexibility in embryo development rates and feeding windows under different warming scenarios (Karjalainen et al. 2015). This only further complicates the downstream impacts autumn, winter, and spring water temperatures may have on embryo and larval phenotypic plasticity. The trade-off between conserving yolk to delay starvation or consuming yolk to grow and feed exogenously is complicated, however, our data shows that population specifics need to be considered when making management decisions.

Traits of embryos and larvae depend not only on population and temperature but also on maternal investment and transgenerational effects (Blaxter 1963, 1991, Kekäläinen et al. 2018). Our results suggest that both maternal and additive genetic effects (*i.e.,* heritability) control a portion of early-stage offspring trait phenotype in coregonines. In many cases, a maternal effect in a trait is high when correlated to egg size (*e.g.,* yolk-sac) and diminishes over time (Green 2008). Heritability and adaptive genetic effects become more apparent after the influence of egg size is diminished (Green 2008). Larger and older females typically produce higher quality eggs and therefore higher quality offspring (Roff 1994, Stewart 2011, Hixon et al. 2014). Our results support differential levels of response between heritability and maternal effects in traits correlated with egg size. Knowing how increases in water temperature may impact the short-term plasticity and transgenerational effects of coregonines is important for understanding the independence between short- and long-term resilience to climate change. For example, increases in water temperature can impact the sperm of European whitefish, shape offspring phenotype, and negatively impact post-hatching larval performance (Kekäläinen et al. 2018). The concept that spawning stocks comprise individuals of a range of sizes and ages that may contribute differently to spawning, offspring performance, and recruitment is an even more important consideration in commercially exploited stocks like coregonines, which may experience fisheries-induced evolution. Sparse knowledge of coregonine genetic and physiological architectures of thermal plasticity limits our ability to predict the transgenerational effect on resilience to the rapid rate of climate and projected increases in their thermal habitat.

Latitudinal Compensation

An additional explanation of latitudinal variation could be a form of latitudinal compensation in various metabolic processes (Conover and Schultz 1995, Wilder et al. 2020). A number of species (*e.g.,* Arctic char *Salvelinus alpinus*, Atlantic cod *Gadus morhua*, Atlantic silversides *Menidia menidia*, Atlantic salmon *Salmo salar*, striped bass *Morone saxatilis*, and turbot *Scophthalmus maximus*) have demonstrated an ﻿inverse relationship between the length of the growing season and life history and morphological trait performance (*i.e.,* countergradient variation; Conover and Present 1990, Conover and Schultz 1995, Schultz et al. 1996, 1998, Billerbeck et al. 2000, Jonassen 2000, Yamahira and Conover 2002, Chavarie et al. 2010, Wilder et al. 2020), where higher-latitude populations have a higher trait performance potential compared with lower-latitude populations. Countergradient variation suggests that higher-latitude populations compensate for a shorter growing season by evolving a higher overall efficiency in specific traits. Empirical support for the countergradient hypothesis demonstrates a widespread phenomenon, and illustrates that geographic variation in traits is a potentially important descriptor of differences among populations. We were not able to test the countergradient hypothesis because the limited number of populations and the geographical discrepancy between continents was concerning in applicability and precision. Our results do suggest that some form of latitudinal variation is present and increasing the number of populations within each continent for future studies may help provide an additional understanding into what is driving latitudinal compensation.

The existence of a latitudinal response also 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). A mechanistic understanding of thermal response across latitudes will be essential to predict the vulnerability of species and populations to climate change.

Early Life in Stressful Environments

Water temperature is fundamental in regulating fish physiology (Little et al. 2020). Coregonine populations at the southern extent of their range have declined and, in some lakes, suffered local extirpations (Anneville et al. 2009, Burkhead 2012, Vonlanthen et al. 2012, Mandrak et al. 2014, Rosinski et al. 2020). Coregonines are the focus of reintroduction, restoration, and conservation efforts given the declines (Favé and Turgeon 2008, Lucke et al. 2020, Rosinski et al. 2020). Climate change, increasing water temperatures, and habitat degradation are hypothesized as causal factors of declining coregonine populations (Jeppesen et al. 2012, Anneville et al. 2015). Lake winter temperatures are rising at an accelerated rate compared to summer (O’Reilly et al. 2015, Woolway et al. 2020), suggesting winter is likely to be the most sensitive season for coregonines. Southern Arctic charr populations in Europe are being negatively affected by rising winter temperatures and both current and projected winter water temperatures exceed 11°C (Kelly et al. 2020) in many lakes at the southern European extent for coregonines.

Environmental variation during development can play a large role in generating variability in offspring through phenotypic plasticity. How coregonines respond, during the critical embryonic and larval stages, is important to determine if the capacity to respond to the rapid rate of climate change and the projected increases in their thermal habitat exists. Knowing how populations have adapted historically to environmental variability will help us understand the future response we may see to climate change and assist managers to ensure coregonines remain out of hot water. Our hope is that this study provides a springboard for future large-scale experimental research on coregonines as we were able to provide evidence that coregonines do exhibit adaptation to latitude and possess a high level of thermal plasticity for some traits, even though this study was limited to three lakes. The methods we developed allow for reproducible and standardized results (*e.g.,* constant water source across locations, no moving water, individual-level measurements, etc.) that can be compared to future experiments as additional work examining temperature responses from a wider range of populations is warranted. Additionally, interpreting the impacts of trait heritability and maternal response within an environmental context continues to be important for determining how parental effects may assist species’ responses to rapid climate change.

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**TABLES:**

Table 1. Mean (SD) water temperatures (°C) during embryo incubations at the University of Vermont (UVM) and University of Jyväskylä (JYU).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | Incubation Temperature Treatment | | | | | | |
| Laboratory | 2.0 |  | 4.5 |  | 7.0 |  | 9.0 |
| 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. Mean (SD) total length (TL; mm) and fresh mass (FM; g) of the dams and sires from Lake Konnevesi (LK-Vendace (*Coregonus albula*) and LK-Whitefish (*C. lavaretus*)), Lake Superior (LS-Cisco (*C. artedi*)), and Lake Ontario (LO-Cisco).

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | LK-Vendace | |  | LK-Whitefish | |  | LS-Cisco | |  | LO-Cisco | |
| Sex | TL | FM |  | TL | FM |  | TL | FM |  | TL | FM |
| 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 3. Likelihood ratio test output for each model selected for embryo survival (%), incubation period (number of days post-fertilization; DPF), and incubation period (accumulated degree-days; ADD) from Lakes Superior and Ontario cisco (*Coregonus artedi*), Lake Konnevesi vendace (*C. albula*), and Lake Konnevesi European whitefish (*C. lavaretus*). t indicates temperature and pop indicates population. The full model that was selected is bolded for each trait and species.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Trait | Species | Model | Effect Tested | df | χ2 | p-value |
| Embryo Survival | Cisco | **t + pop + t:pop + dam:sire + dam** |  |  |  |  |
|  | pop + dam:sire + dam | t | 3 | 443.54 | < 0.001 |
|  |  | t + dam:sire + dam | pop | 1 | 600.61 | < 0.001 |
|  |  | t + pop + dam:sire + dam | t:pop | 3 | 198.56 | < 0.001 |
|  |  | t + pop + t:pop + dam | dam:sire | 1 | 181.47 | < 0.001 |
|  |  | t + pop + t:pop + dam:sire | dam | 1 | 23.36 | < 0.001 |
|  | Vendace | **t + dam:sire + dam** |  |  |  |  |
|  |  | dam:sire + dam | t | 3 | 77.03 | < 0.001 |
|  |  | t + dam | dam:sire | 1 | 49.55 | < 0.001 |
|  |  | t + dam:sire | dam | 1 | 16.58 | < 0.001 |
|  | Whitefish | **t + dam:sire + dam + sire** |  |  |  |  |
|  |  | dam:sire + sire + dam | t | 3 | 165.26 | < 0.001 |
|  |  | t + sire + dam | dam:sire | 1 | 5.94 | 0.015 |
|  |  | t + dam:sire + sire | dam | 1 | 3.63 | 0.057 |
|  |  | t + dam:sire + dam | sire | 1 | 18.83 | < 0.001 |
| Incubation Period (DPF) | Cisco | **t + pop + t:pop + dam:sire + dam + sire** |  |  |  |  |
|  | pop + dam:sire + dam + sire | t | 3 | 27,176.01 | < 0.001 |
|  | t + dam:sire + dam + sire | pop | 1 | 3,173.76 | < 0.001 |
|  |  | t + pop + dam:sire + dam + sire | t:pop | 3 | 1,113.95 | < 0.001 |
|  |  | t + pop + t:pop + dam + sire | dam:sire | 1 | 64.82 | < 0.001 |
|  |  | t + pop + t:pop + dam:sire + sire | dam | 1 | 60.90 | < 0.001 |
|  |  | t + pop + t:pop + dam:sire + dam | sire | 1 | 8.59 | 0.003 |
|  | Vendace | **t + dam + sire** |  |  |  |  |
|  |  | dam + sire | t | 3 | 6,644.13 | < 0.001 |
|  |  | t + sire | dam | 1 | 229.13 | < 0.001 |
|  |  | t + dam | sire | 1 | 33.66 | < 0.001 |
|  | Whitefish | **t + dam:sire + dam** |  |  |  |  |
|  |  | dam:sire + dam | t | 3 | 1,777.27 | < 0.001 |
|  |  | t + dam | dam:sire | 1 | 13.07 | < 0.001 |
|  |  | t + dam:sire | dam | 1 | 7.16 | 0.007 |
| Incubation Period (ADD) | Cisco | **t + pop + t:pop + dam:sire + dam + sire** |  |  |  |  |
|  | pop + dam:sire + dam + sire | t | 3 | 14,370.19 | < 0.001 |
|  | t + dam:sire + dam + sire | pop | 1 | 3,495.26 | < 0.001 |
|  |  | t + pop + dam:sire + dam + sire | t:pop | 3 | 160.60 | < 0.001 |
|  |  | t + pop + t:pop + dam + sire | dam:sire | 1 | 61.35 | < 0.001 |
|  |  | t + pop + t:pop + dam:sire + sire | dam | 1 | 60.90 | < 0.001 |
|  |  | t + pop + t:pop + dam:sire + dam | sire | 1 | 14.08 | < 0.001 |
|  | Vendace | **t + dam:sire + dam + sire** |  |  |  |  |
|  |  | dam:sire + dam + sire | t | 3 | 3,753.05 | < 0.001 |
|  |  | t + dam + sire | dam:sire | 1 | 4.19 | 0.041 |
|  |  | t + dam:sire + sire | dam | 1 | 40.10 | < 0.001 |
|  |  | t + dam:sire + dam | sire | 1 | 5.62 | 0.018 |
|  | Whitefish | **t + dam:sire + dam** |  |  |  |  |
|  |  | dam:sire + dam | t | 3 | 719.36 | < 0.001 |
|  |  | t + dam | dam:sire | 1 | 15.76 | < 0.001 |
|  |  | t + dam:sire | dam | 1 | 6.63 | 0.010 |

Table 4. Likelihood ratio test output for each model selected for length-at-hatch (mm) and yolk-sac volume (mm3) from Lakes Superior and Ontario cisco (*Coregonus artedi*), Lake Konnevesi vendace (*C. albula*), and Lake Konnevesi European whitefish (*C. lavaretus*). t indicates temperature and pop indicates population. The full model that was selected is bolded for each trait and species.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Trait | Species | Model | Effect Tested | df | χ2 | p-value |
| Length-at-Hatch | Cisco | **t + pop + dam** |  |  |  |  |
|  | pop + dam | t | 3 | 894.52 | < 0.001 |
|  |  | t + dam | pop | 1 | 593.34 | < 0.001 |
|  |  | t + pop | dam | 1 | 103.91 | < 0.001 |
|  | Vendace | **t + dam + sire** |  |  |  |  |
|  |  | dam + sire | t | 3 | 444.27 | < 0.001 |
|  |  | t + sire | dam | 1 | 234.82 | < 0.001 |
|  |  | t + dam | sire | 1 | 29.24 | < 0.001 |
|  | Whitefish | **t + dam:sire + dam** |  |  |  |  |
|  |  | dam:sire + dam | t | 3 | 108.29 | < 0.001 |
|  |  | t + dam | dam:sire | 1 | 18.90 | < 0.001 |
|  |  | t + dam:sire | dam | 1 | 18.00 | < 0.001 |
| Yolk-sac Volume | Cisco | **t + pop + t:pop + dam** |  |  |  |  |
|  | pop+ dam | t | 3 | 1,041.57 | < 0.001 |
|  |  | t + dam | pop | 1 | 142.63 | < 0.001 |
|  |  | t + pop + dam | t:pop | 3 | 36.46 | < 0.001 |
|  |  | t + pop + t:pop | dam | 1 | 332.96 | < 0.001 |
|  | Vendace | **t + dam:sire + dam** |  |  |  |  |
|  |  | dam:sire + dam | t | 3 | 652.37 | < 0.001 |
|  |  | t + dam | dam:sire | 1 | 9.35 | 0.002 |
|  |  | t + dam:sire | dam | 1 | 19.39 | < 0.001 |
|  | Whitefish | **t + dam + sire** |  |  |  |  |
|  |  | dam + sire | t | 3 | 300.26 | < 0.001 |
|  |  | t + sire | dam | 1 | 26.34 | < 0.001 |
|  |  | t + dam | sire | 1 | 3.06 | 0.080 |

Table 5. Bootstrap bias-corrected median narrow-sense heritability (h2 ± SE) and nongenetic maternal (m2 ± SE) estimates with number of individuals used (N) for embryo survival (%), incubation period (number of days post-fertilization; DPF), and incubation period (accumulated degree-days; ADD) from Lake Konnevesi (LK-Vendace (*Coregonus albula*)), Lake Superior (LS-Cisco (*C. artedi*)), and Lake Ontario (LO-Cisco) across each incubation temperature treatment (°C).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Trait | Population | Incubation Temperature | h2 ± SE | m2 ± SE | N |
| Embryo Survival | LK-Vendace | 2.2 | 0.10 ± 0.11 | 0.19 ± 0.08 | 667 |
|  | 4.0 | 0.00 ± 0.05 | 0.08 ± 0.04 | 985 |
|  |  | 6.9 | 0.21 ± 0.11 | 0.11 ± 0.07 | 961 |
|  |  | 8.0 | 0.19 ± 0.09 | 0.02 ± 0.03 | 994 |
|  | LS-Cisco | 2.0 | 0.00 ± 0.05 | 0.32 ± 0.07 | 916 |
|  |  | 4.4 | 0.00 ± 0.07 | 0.47 ± 0.04 | 856 |
|  |  | 6.9 | 0.00 ± 0.14 | 0.33 ± 0.12 | 892 |
|  |  | 8.9 | 0.00 ± 0.04 | 0.11 ± 0.04 | 836 |
|  | LO-Cisco | 2.0 | 0.00 ± 0.10 | 0.17 ± 0.17 | 2043 |
|  |  | 4.4 | 0.00 ± 0.24 | 0.30 ± 0.25 | 2012 |
|  |  | 6.9 | 0.00 ± 0.08 | 0.19 ± 0.08 | 2022 |
|  |  | 8.9 | 0.18 ± 0.06 | 0.10 ± 0.03 | 1987 |
| Incubation Period (DPF) | LK-Vendace | 2.2 | 0.07 ± 0.06 | 0.16 ± 0.04 | 667 |
|  | 4.0 | 0.22 ± 0.08 | 0.07 ± 0.04 | 985 |
|  |  | 6.9 | 0.00 ± 0.04 | 0.17 ± 0.04 | 961 |
|  |  | 8.0 | 0.02 ± 0.05 | 0.42 ± 0.05 | 994 |
|  | LS-Cisco | 2.0 | 0.00 ± 0.04 | 0.41 ± 0.04 | 916 |
|  |  | 4.4 | 0.19 ± 0.07 | 0.21 ± 0.04 | 856 |
|  |  | 6.9 | 0.26 ± 0.10 | 0.12 ± 0.05 | 892 |
|  |  | 8.9 | 0.14 ± 0.12 | 0.02 ± 0.04 | 836 |
|  | LO-Cisco | 2.0 | 0.27 ± 0.02 | 0.46 ± 0.02 | 2043 |
|  |  | 4.4 | 0.38 ± 0.03 | 0.30 ± 0.02 | 2012 |
|  |  | 6.9 | 0.22 ± 0.03 | 0.37 ± 0.02 | 2022 |
|  |  | 8.9 | 0.12 ± 0.04 | 0.26 ± 0.03 | 1987 |
| Incubation Period (ADD) | LK-Vendace | 2.2 | 0.13 ± 0.09 | 0.13 ± 0.05 | 667 |
|  | 4.0 | 0.22 ± 0.09 | 0.07 ± 0.04 | 985 |
|  |  | 6.9 | 0.00 ± 0.04 | 0.17 ± 0.04 | 961 |
|  |  | 8.0 | 0.00 ± 0.04 | 0.42 ± 0.04 | 994 |
|  | LS-Cisco | 2.0 | 0.00 ± 0.04 | 0.41 ± 0.04 | 916 |
|  |  | 4.4 | 0.19 ± 0.07 | 0.21 ± 0.04 | 856 |
|  |  | 6.9 | 0.26 ± 0.10 | 0.12 ± 0.05 | 892 |
|  |  | 8.9 | 0.14 ± 0.11 | 0.02 ± 0.04 | 836 |
|  | LO-Cisco | 2.0 | 0.28 ± 0.03 | 0.44 ± 0.02 | 2043 |
|  |  | 4.4 | 0.38 ± 0.03 | 0.30 ± 0.02 | 2012 |
|  |  | 6.9 | 0.22 ± 0.03 | 0.37 ± 0.02 | 2022 |
|  |  | 8.9 | 0.12 ± 0.04 | 0.26 ± 0.03 | 1987 |

Table 6. Bootstrap bias-corrected median narrow-sense heritability (h2 ± SE) and nongenetic maternal (m2 ± SE) estimates with number of individuals used (N) for length-at-hatch (mm) and yolk-sac volume (mm3) from Lake Konnevesi (LK-Vendace (*Coregonus albula*)), Lake Superior (LS-Cisco (*C. artedi*)), and Lake Ontario (LO-Cisco) across each incubation temperature treatment (°C).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Trait | Population | Incubation Temperature | h2 ± SE | m2 ± SE | N |
| Length-at-Hatch | LK-Vendace | 2.2 | 0.35 ± 0.15 | 0.12 ± 0.09 | 176 |
|  | 4.0 | 0.31 ± 0.12 | 0.18 ± 0.08 | 180 |
|  |  | 6.9 | 0.00 ± 0.02 | 0.47 ± 0.06 | 180 |
|  |  | 8.0 | 0.23 ± 0.15 | 0.23 ± 0.10 | 180 |
|  | LS-Cisco | 2.0 | 0.04 ± 0.08 | 0.56 ± 0.08 | 136 |
|  |  | 4.4 | 0.00 ± 0.04 | 0.27 ± 0.10 | 132 |
|  |  | 6.9 | 0.00 ± 0.42 | 0.37 ± 0.19 | 120 |
|  |  | 8.9 | 0.00 ± 0.44 | 0.42 ± 0.12 | 110 |
|  | LO-Cisco | 2.0 | 0.00 ± 0.09 | 0.29 ± 0.07 | 240 |
|  |  | 4.4 | 0.00 ± 0.05 | 0.11 ± 0.06 | 235 |
|  |  | 6.9 | 0.00 ± 0.27 | 0.37 ± 0.17 | 235 |
|  |  | 8.9 | 0.00 ± 0.18 | 0.00 ± 0.20 | 228 |
| Yolk-sac Volume | LK-Vendace | 2.2 | 0.00 ± 0.03 | 0.11 ± 0.08 | 176 |
|  | 4.0 | 0.23 ± 0.16 | 0.11 ± 0.09 | 180 |
|  |  | 6.9 | 0.00 ± 0.12 | 0.39 ± 0.09 | 180 |
|  |  | 8.0 | 0.04 ± 0.12 | 0.41 ± 0.09 | 180 |
|  | LS-Cisco | 2.0 | 0.00 ± 0.02 | 0.28 ± 0.10 | 136 |
|  |  | 4.4 | 0.00 ± 0.11 | 0.39 ± 0.09 | 132 |
|  |  | 6.9 | 0.00 ± 0.04 | 0.44 ± 0.09 | 120 |
|  |  | 8.9 | 0.00 ± 0.03 | 0.04 ± 0.07 | 110 |
|  | LO-Cisco | 2.0 | 0.00 ± 0.09 | 0.38 ± 0.07 | 240 |
|  |  | 4.4 | 0.05 ± 0.07 | 0.51 ± 0.07 | 235 |
|  |  | 6.9 | 0.00 ± 0.02 | 0.40 ± 0.05 | 235 |
|  |  | 8.9 | 0.00 ± 0.14 | 0.32 ± 0.09 | 228 |

**FIGURES:**

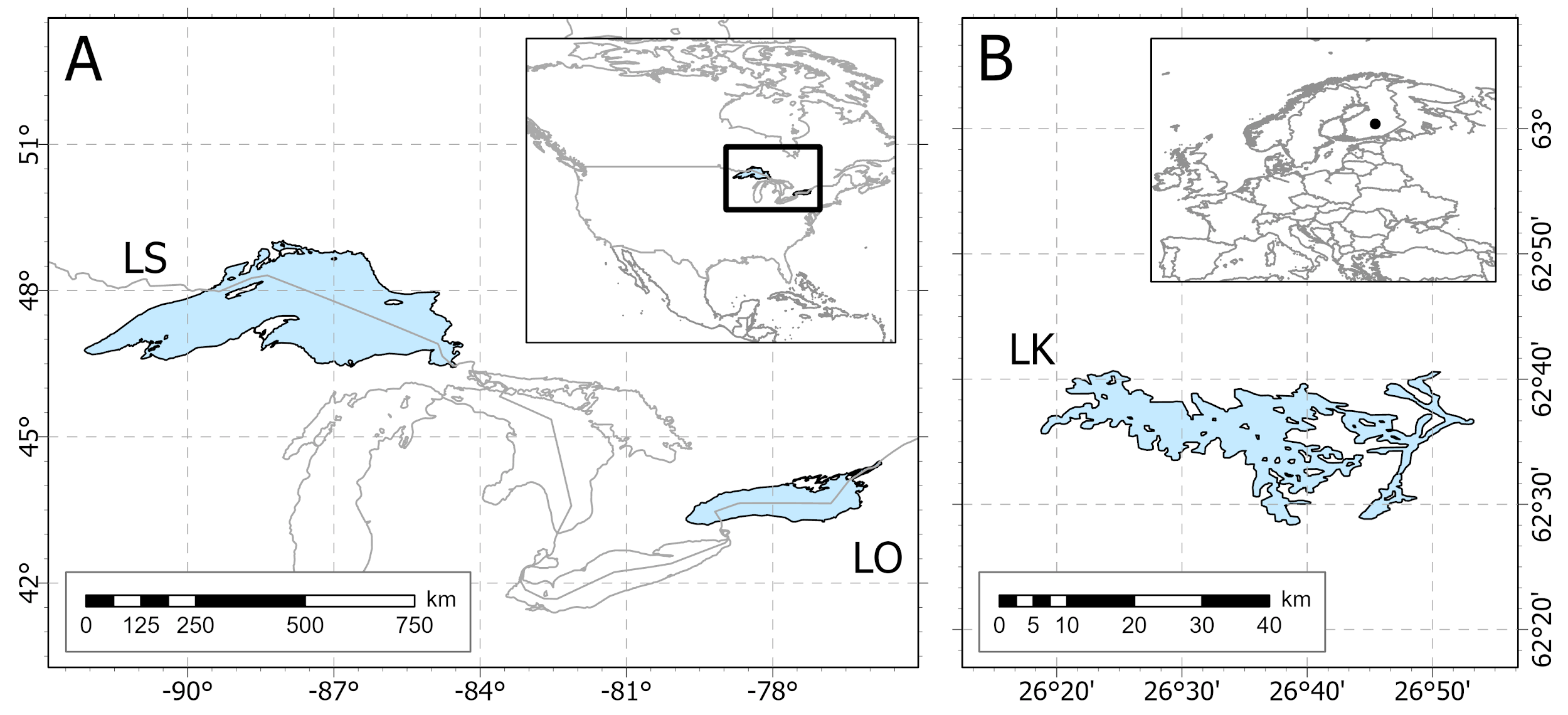


Figure 1. Map showing the location of each lake (LS = Lake Superior; LO = Lake Ontario; LK = Lake Konnevesi) sampled in North America (A) and Europe (B).

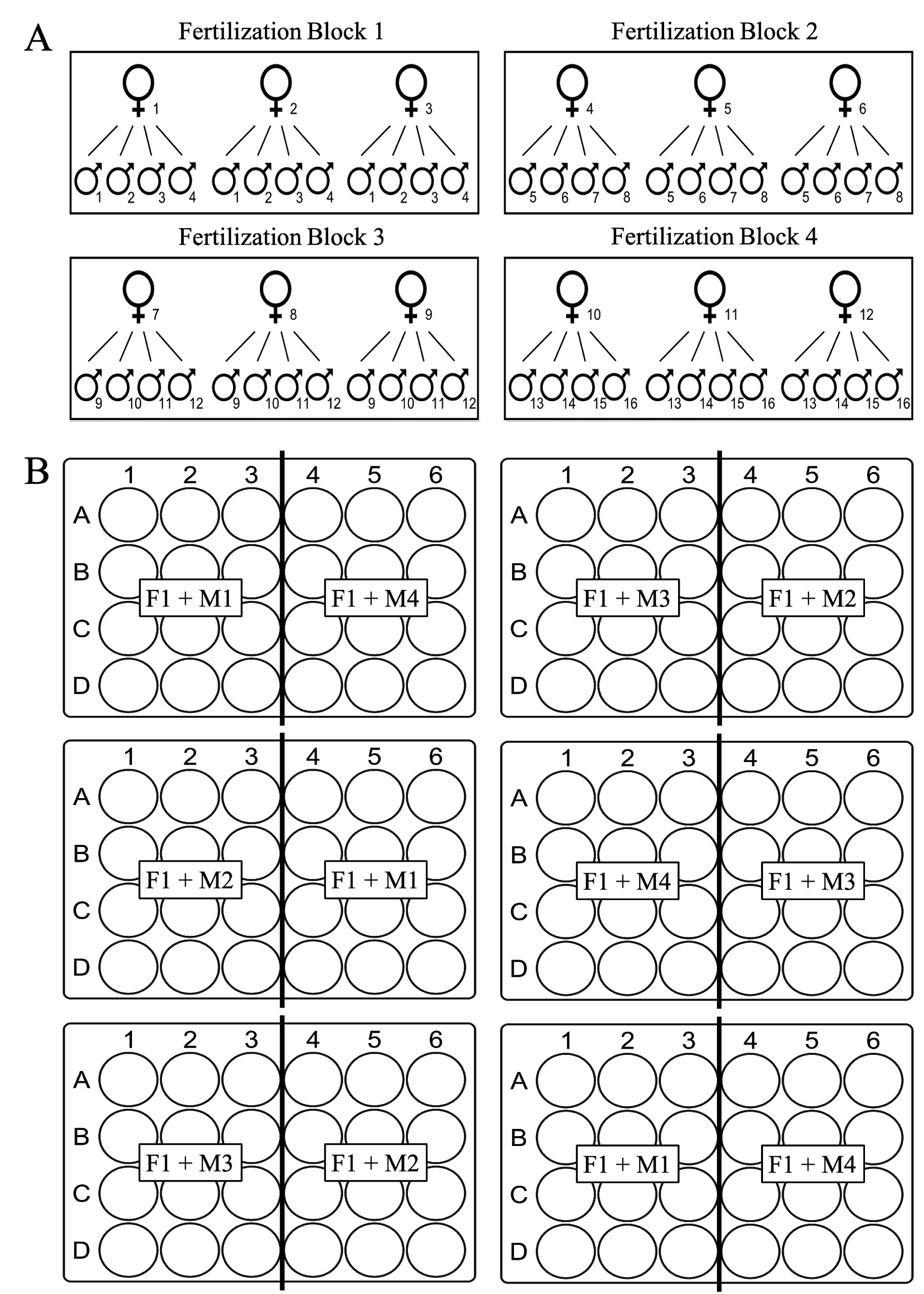


Figure 2. Crossbreeding design (A) and a theoretical division of families from a single female into microplates (B) when the number of offspring equals 36.

Chart

Description automatically generated

Figure 3. Mean embryo survival (%; ES), incubation period (number of days post-fertilization; DPF), and incubation period (accumulated degree day (°C); ADD) at each incubation temperature (°C) from Lake 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.

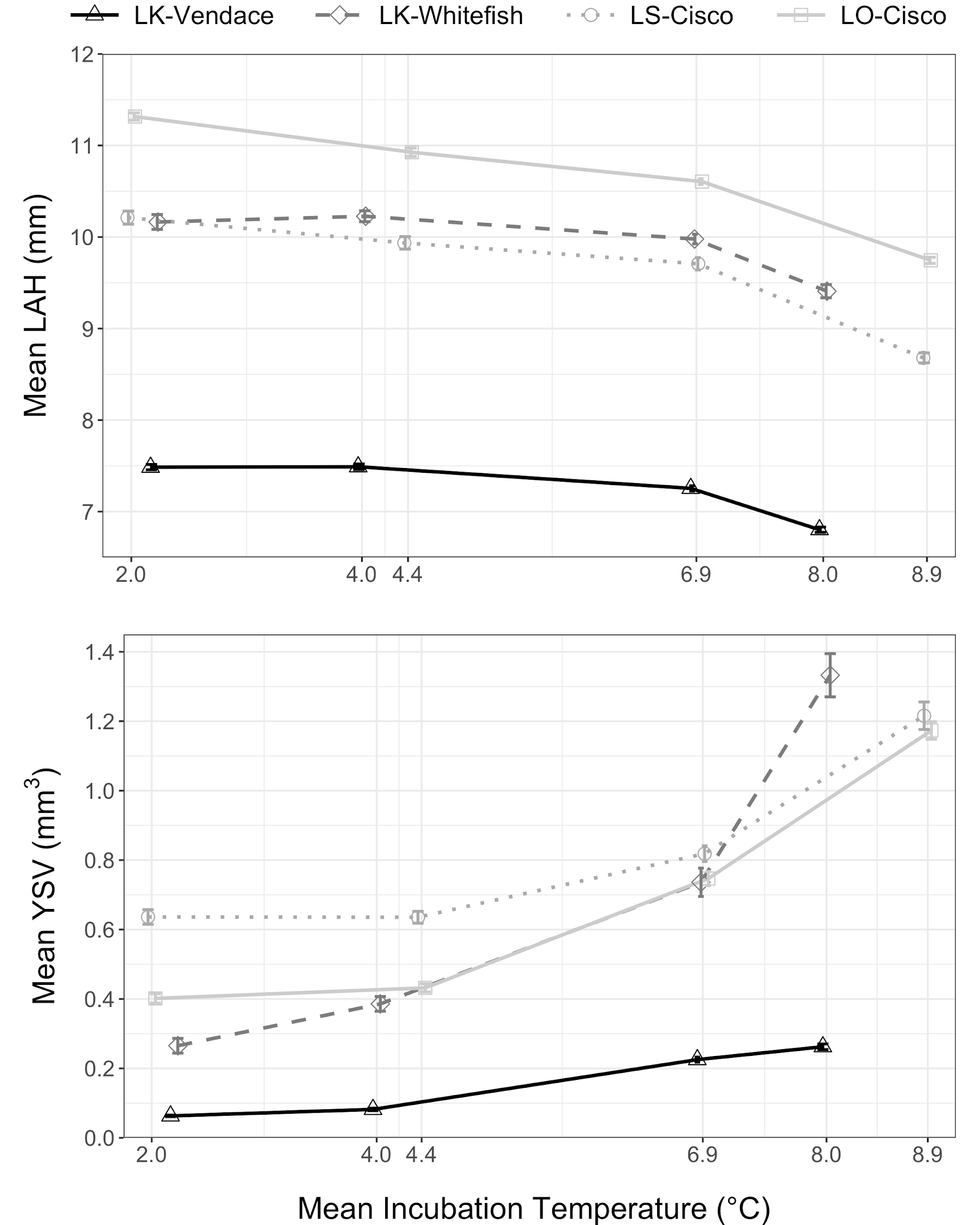


Figure 4. Mean length-at-hatch (LAH) and yolk-sac volume (YSV) at each incubation temperature (°C) from Lake Konnevesi (LK-Vendace (*Coregonus albula*) and LK-Whitefish (*C. lavaretus*)), Lake Superior (LS-Cisco (*C. artedi*)), and Lake Ontario (LO-Cisco). Error bars indicate standard error.

Graphical user interface, chart, line chart

Description automatically generated

Figure 5. Theoretical winter incubation periods 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) for cisco (*Coregonus artedi*) that typically occur between 3-4°C. The 2.0°C temperature regime is water temperature data collected from Lake Superior at 10-m depth in 2018.