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

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**ABSTRACT:**

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**INTRODUCTION:**

Aquatic ecosystems present unique and difficult challenges for biodiversity conservation because of the diverse array of habitats and the numerous socio-economic benefits they provide (Halpern et al. 2015, Langhans et al. 2019). Lakes are one of the most sensitive natural resources to climate change (Woolway et al. 2020). Climate change can alter lake physical and chemical characteristics and has biological consequences for lake ecology and metabolism(Adrian et al. 2009, Williamson et al. 2014), yet the broader impacts of climate-derived changes in lake dynamics remain unclear (Shatwell et al. 2019). However, the responses of many lake populations are projected to be inadequate to counter the speed and magnitude of climate change, leaving groups vulnerable to decline and extinction (Hoffmann and Sgrò 2011).

Lakes are warming 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 steadily 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 will be during winter in northern Europe and North America (Christensen et al. 2007). Changes in spring conditions and increases in 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). 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 climate change on lake fishes are predicted to lead to declines in cold-water species (Fang et al. 2004, Mackenzie-Grieve and Post 2006, Jacobson et al. 2010, Herb et al. 2014) and increases in warm-water species (Lehtonen 1996, Chu et al. 2005, Sharma et al. 2007, Van Zuiden et al. 2016) as the climate warms (Comte et al. 2013, Hansen et al. 2017). ﻿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, Lynch et al. 2015, 2016). Coregonines 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). 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 on embryos (Blaxter 1991, Pepin 1991, Ficke et al. 2007, Lim et al. 2017). 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 reason for declining recruitment is 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). Spawning adults, embryos, and larvae are exposed to a variety of thermal conditions throughout this long period of reproduction and incubation. 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).

Life history traits in fishes can vary across latitudes and the driving selective force for this variation is size-dependent winter mortality in young-of-the-year (Conover and Present 1990, Yamahira and Conover 2002, Chavarie et al. 2010). ﻿Such size-dependent winter mortality results in a strong and increasing selection pressure towards fast-growing fishes with increasing latitude. Year-class strength of most fish species, including coregonines, is thought to be established prior to the end of the first season of growth, with the first few weeks after hatching especially critical (Hjort 1914, Cushing 1990, Ludsin et al. 2011, 2014, Karjalainen et al. 2015, 2016). The response of coregonines to environmental change at the embryonic and larval stages are expected to play an important role in population persistence (Myers 1997, Karjalainen et al. 2000) and have major implications on ecosystem health as coregonines contribute significantly to ecosystem function and energy transfer (Gamble et al. 2011, Muir et al. 2014, Stockwell et al. 2014, Karjalainen et al. 2015). Large-scale experimental evolution studies may aid in understanding the response of coregonines to changing environments (Hoffmann and Sgrò 2011). 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 parameters, such as water temperature.

We experimentally analyzed the reaction norms of early-life stage coregonines to changing winter thermal regimes across broad latitudinal gradients. We hypothesized that coregonine populations across latitudes will have differential responses to changing winter conditions. Evolutionary differences to varying climates may be driving thermal resilience during embryonic and larval stages. High-latitude populations which experience lower water temperatures and longer winters 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 than populations at lower latitudes. We also hypothesized that a greater magnitude of seasonal fluctuations and water temperature variation will result in lower-latitude populations having a stronger parental response to changing temperatures due to stronger selection towards thermal plasticity. Understanding the adaptive capacity of coregonine populations will be critical to determining which populations may survive and which may perish as thermal conditions continue to change.

**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 in Lake Superior (USA/Canada) and Lake Ontario (USA/Canada), and vendace and European 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 = 2.80°C, sd = 0.21°C; Lake Ontario: mean = 3.28°C, sd = 0.37°C). 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

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

*Life-history and Morphological Traits*

Embryo survival (ES) 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 (DPF) and the sum of the degree-days (ADD). Total length-at-hatch (LAH; 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. YSV 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, LAH, and YSV 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 ES and subsequently resulted in an unbalanced design. Therefore, binary data (*i.e.,* ES) were analyzed with binomial generalized linear mixed-effects models (LMM) and normally distributed data (*i.e.,* DPF, ADD, LAH, and YSV) 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. Lake Superior and Lake Ontario cisco (hereafter Great Lakes region (GLR)) were fit independently from Lake Konnevesi vendace and European whitefish (hereafter Finland region (FIR) to eliminate any confounding factors between continents.

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*Parental Response*

In addition to population-level effects, life-history and morphological traits were analyzed for heritability. 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, nongenetic 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.

**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 7.0°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. Lake Konnevesi vendace were notably smaller than all other populations. The remaining populations varied less in size, but Lake Konnevesi whitefish were smaller than Lake Superior cisco and Lake Ontario cisco. The size of spawning adults decreased as latitude increases and was different between regions (*i.e.,* continents) and among species (Table 2).

Life-history and Morphological Traits

*Embryo Survival*

The likelihood-ratio test found significant interaction effects between ES in population and incubation temperature for both GLR (*P* < 0.001, χ2 = 198.56, 3 df) and FIR lakes (*P* < 0.001, χ2 = 52.94, 3 df; Table 3) and does not allow for main effect interpretation. The effect of population depended on temperature because the ﻿differences in ES among populations were more pronounced at higher temperatures. ES was highest among all populations at 2.0°C. LO-Cisco had the highest ES up to 7.0°C and then decreased rapidly at 9.0°C. LS-Cisco and LK-Vendace ES was less variable across all temperatures, but less than LO-Cisco. ES in LK-Whitefish was lowest among populations and consistently decreased as temperature increased (Figure 2).

*Incubation Period (DPF)*

The likelihood-ratio test found significant interaction effects between DPF in population and incubation temperature for both GLR (*P* < 0.001, χ2 = 1,113.95, 3 df) and FIR lakes (*P* < 0.001, χ2 = 157.91, 3 df; Table 3) and does not allow for main effect interpretation. ﻿The effect of population depended on temperature because the ﻿differences in DPF among populations were more pronounced at colder temperatures. DPF 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 2).

*Incubation Period (ADD)*

The likelihood-ratio test found significant interaction effects between ADD in population and incubation temperature for both GLR (*P* < 0.001, χ2 = 160.60, 3 df) and FIR lakes (*P* < 0.001, χ2 = 440.18, 3 df; Table 3) and does not allow for main effect interpretation. The effect of population depended on temperature because the ﻿differences in ADD among populations were more pronounced at higher temperatures. ADD was highest for all populations at 7.0°C and decreased as temperature increased and decreased. Higher-latitude populations (*i.e.,* LK-Vendace and LK-Whitefish) had larger differences in incubation periods across temperature compared to lower-latitude populations (*i.e.,* LS-Cisco and LO-Cisco; Figure 2).

*Length-at-Hatch*

The likelihood-ratio test found a significant interaction effect between LAH in population and incubation temperature in FIR lakes (*P* = 0.031, χ2 = 8.85, 3 df; Table 4) and does not allow for main effect interpretation. Both temperature (*P* < 0.001, χ2 = 592.28, 3 df) and population (*P* < 0.001, χ2 = 443.20, 1 df; Table 4) main effects were significant in GLR lakes. All pairwise population and temperature comparisons for both GLR lakes were significant (*P* < 0.001). All populations showed a decrease in LAH as temperature increased. LO-Cisco had the largest LAH across all temperatures. LK-Vendace had a large difference in LAH and were significantly smaller compared to all other populations.

*Yolk-sac Volume*

The likelihood-ratio test found significant interaction effects between YSV in population and incubation temperature for both GLR (*P* < 0.001, χ2 = 36.50, 3 df) and FIR lakes (*P* < 0.001, χ2 = 157.91, 3 df; Table 4) and does not allow for main effect interpretation. YSV was highest for all populations at 9.0°C and decreased as temperature decreased. LK-Vendace had a large difference in YSV and was significantly smaller compared to all other populations. Excluding LK-Vendace, YSV 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; Figure 3). The difference in YSV between GLR populations decreased as temperature increased.

Parental Response

The dam effect was significant in all life-history and morphological traits, and the sire effect was significant for DPF and ADD in both FDR and GLR populations, and YSV in FIR populations (Tables 3 and 4). Heritability estimates in life history and morphological traits in response to temperature was moderate (< 0.40). Embryo survival and yolk-sac volume showed the lowest degree of heritability across all populations (Tables 5 and 6). Incubation period (both DPF and ADD) had the highest heritability, with LO-Cisco and LK-Vendace having the highest response at colder temperatures and LS-Cisco at the warmer temperatures (Table 5). Length-at-hatch heritabilities were variable and showed high amounts error in the estimates (Table 6).

The relative importance of the maternal variance was examined and was found to be a moderate portion of the phenotypic variance (< 0.60). Maternal effect was most consistent among populations for morphological traits (Table 6). Incubation period (both DPF and ADD) showed opposing trends in the maternal effect between GLR and FIR populations. GLR populations had higher maternal effects at colder temperatures with LO-Cisco always higher than LO-Cisco. LK-Vendace DPF and ADD showed low maternal effects at cold temperatures and a rapid increase at 9.0°C (Table 5).

**DISCUSSION:**

We studied the impact of climate-induced increases to winter water temperature on coregonine embryo incubations from different populations in North America and Europe. We tested whether there are population differences in the response and parental effect for thermal tolerance. Our results demonstrate substantial latitudinal variation in reaction norms for both life-history and morphological traits in response to temperature for coregonines.

Life-history Traits

Embryo survival was the only life-history and morphological trait that did not exhibit some form of latitudinal gradient to temperature. The response to temperature for ES was intraspecies as there was a consistent pattern across populations and did not appear to be influenced by latitude (Figure X). While temperature is thought to be the main force determining ES, all populations, except LK-Whitefish, saw relatively high survival rates across all temperature treatments regardless of any local adaptation to winter temperatures. The greatest decrease in ES between the coldest and warmest treatments was in LO-Cisco, our southernmost population, suggesting that southern populations may have the strongest negative response in embryo survival from rising temperatures (Figure X). Incubation period showed the largest response to temperature across the latitudinal gradient. In particular, LK-Vendace had the longest incubation periods, even when exposed to high temperatures (*i.e.,* high ADD), suggesting a high degree of local adaptation towards long incubation periods. LK-Whitefish incubation periods showed a similar, but lesser, response to temperature. All populations began showing a decrease in ADD and ES after 7.0°C suggesting that this may be a temperature inflection point where populations will begin to show a strong adverse effect during incubations from temperatures beyond that point (Figure X).

The incubation period response to temperature was particularly interesting as high-latitude populations typically spawn earlier in autumn and may have the opportunity to shift timing of reproduction, while still providing an adequate incubation period for embryo development, as temperatures increase. 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 temperatures and do not have the thermal plasticity to withstand high temperatures. This potentially opens the question of is there an adaptive opportunity for southern populations to have a subsequent spawning event peak later in the winter and have a spring spawning population if temperatures continue to rise? Spring spawning populations may leave 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. If winter water temperatures continue to rise, coregonine ovulation could be inhibited entirely. Lake morphology would be important to consider alongside this question as deeper lakes could provide colder thermal refuge at greater depths if suitable spawning habitat is available.

Morphological Traits

Length-at-hatch had a uniform response to temperature among populations across the latitudinal gradient as all populations decreased in LAH as temperature increased. However, FIR and GLR have different degrees of declining LAH with rising temperatures. Both species from FIR had approximately the same LAH from 2.0-7.0°C with a sharp decrease at 8.0°C. In contrast, both cisco populations in GLR had a constant decline in LAH from 2.0-9.0°C. The different slopes between FIR and GLR suggests that higher- and lower-latitude populations may have differential responses to temperature with southern populations being affected more than northern populations. This differential response is likely confounded with the different responses shown in incubation periods and directly influenced by the amount of time the embryos were able to develop. Contrary to LAH, YSV had a strong response to temperature among populations across latitudes. YSV in the GLR diverged between the two populations as temperature decreased, but the difference in LAH at each temperature treatment was the same suggesting that YSV is impacted by temperature more than LAH. YSV in LK-Whitefish had a similar trend but to a greater magnitude suggesting a higher sensitivity to temperature. Traits of eleuthero-embryos, like LAH and YSV, depend not only on population and temperature but also on egg size and maternal investment (Blaxter 1963, 1991). The size of spawning vendace from Lake Konnevesi were smaller than other populations and the females had smaller eggs in general. This paternal difference is likely the cause of YSV and LAH being smaller across all temperatures compared to all other populations.

The trade-off between LAH and YSV is clearly documented in larval fish physiology (Blaxter 1991). The challenge for managers making conservation decisions with regards to temperature adaptation in coregonines is to determine what trait is more important. LAH and YSV are negatively correlated and can have large implications on larval survival. Conserving your yolk-sac during development will extend endogenous feeding and delay starvation after hatching. However, species with long incubation periods often mature before hatching and require yolk to sustain metabolic demands and somatic growth. Hatching at a larger size allows larvae to swim more effectively and 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 considering the relatively importance of each 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. The trade-off between conserving yolk to delay starvation or consuming yolk to grow and feed exogenously is complicated and our data shows that population specifics need to be considered when making management decisions.

Parental Response

The moderate levels of heritability, or proportion of additive genetic phenotypic variance, and maternal effects, or non-genetic contribution from the mother’s phenotype, show the importance of examining phenotypic variation in offspring when interpreting trait performance under climate change. In many cases, a maternal effect in a trait diminishes with time, as the main maternal influence was on egg size. Paternal effect and additive genetic variation become more apparent after the major egg size influence is diminished (REF). Examining the two sources of phenotypic variation is important to understand offspring success. Our study showed low levels of heritability but higher levels of maternal effects for ES, LAH, and YSV; three traits highly correlated to egg size. However, incubation period (both DPF and ADD) had moderate levels of heritability and maternal effects suggesting that both maternal effects and genotype control a portion of this trait performance. Traditionally, fisheries managers assessed whole populations without regard to size and age variation between individuals within the population (REF). In doing so, the variation in spawning production between individual adults as a source of recruitment variation is overlooked. Larger and older females typically produce higher quality eggs and therefore higher quality offspring (REFS). The concept that spawning stocks are composed of 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 heavily exploited stocks like coregonines.

Latitudinal Compensation

An additional explanation of latitudinal variation could be a form of latitudinal compensation in various metabolic processes (REFS). 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), 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 gradient here also raises questions concerning possible causal mechanisms. Molecular studies will be needed to gain a greater understanding of 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. However, the physiological responses within individuals can still be informative and scale up to population-level responses to climate change.

Early Life in Stressful Environments

Within freshwater lakes, water temperature is fundamental for fish physiology (REFS). Coregonine populations at the southern extent of their range have seen considerable declines and, in some lakes, suffered local extirpations (REFS). Coregonines are the focus of reintroduction, restoration, and conservation efforts given the declines (REFS). Climate change, increasing water temperatures, and habitat degradation have been suggested as possible causal factors to declining coregonine populations (REFS). Lake winter temperatures have been shown to be rising at an accelerated rate compared to summer (O’Reilly et al. 2015, Woolway et al. 2020) suggesting that winter is likely to be the most sensitive season for coregonines. A recent study has shown an imminent threat to southern Arctic charr populations in Europe and both current and projected winter water temperatures exceeding 11°C (Kelly et al. 2020) in many lakes that coregonines share a southern European extent with.

Environmental variation during development can play a large role in generating variability in offspring phenotypes through developmental plasticity. It is important to determine whether embryonic and larval coregonines have the capacity to respond to the rapid rate of climate change and the projected increases in their thermal habitat. Gaining a greater understanding of how populations have adapted historically to environmental variability will help us understand the future response we may see to climate change. Although our study was limited to three lakes, this work still provides evidence that coregonines do exhibit adaptation to latitude and possess a high level of thermal plasticity. Future work examining temperature responses from a wider range of populations is warranted. Additionally, interpreting the impacts of trait heritability and paternal response within an environmental context continues to be highly important for determining how maternal effects may assist species’ responses to rapid climate change.

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**TABLES:**

Table 1. Mean water temperatures (°C) with standard deviations (in parentheses) during embryo incubations at the University of Vermont (UVM) and the 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 total lengths (TL; mm) and fresh mass (FM; g) with standard deviations (in parentheses) 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 the Great Lakes region (GLR; Lake Superior cisco (*Coregonus artedi*) and Lake Ontario cisco) and Finland region (FIR; Lake Konnevesi vendace (*C. albula*) and European whitefish (*C. lavaretus*)). The full model that was selected is bolded for each trait and region.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Trait | Region | Model | Effect Tested | df | χ2 | p-value |
| Embryo Survival | Great Lakes | **t + pop + t:pop + family + dam** |  |  |  |  |
|  | pop + family + dam | t | 3 | 443.54 | < 0.001 |
|  | t + family + dam | pop | 1 | 600.61 | < 0.001 |
|  | t + pop + family + dam | t:pop | 3 | 198.56 | < 0.001 |
|  | t + pop + t:pop + dam | family | 1 | 181.47 | < 0.001 |
|  | t + pop + t:pop + family | dam | 1 | 23.36 | < 0.001 |
| Finland | **t + pop + t:pop + family + dam** |  |  |  |  |
|  | pop + family + dam | t | 3 | 223.54 | < 0.001 |
|  | t + family + dam | pop | 1 | 993.43 | < 0.001 |
|  | t + pop + family + dam | t:pop | 3 | 52.94 | < 0.001 |
|  | t + pop + t:pop + dam | family | 1 | 48.43 | < 0.001 |
|  | t + pop + t:pop + family | dam | 1 | 13.52 | < 0.001 |
| Incubation Period (DPF) | Great Lakes | **t + pop + t:pop + family + dam + sire** |  |  |  |  |
|  | pop + family + dam + sire | t | 3 | 27,176.01 | < 0.001 |
|  | t + family + dam + sire | pop | 1 | 3,173.76 | < 0.001 |
|  | t + pop + family + dam + sire | t:pop | 3 | 1,113.95 | < 0.001 |
|  | t + pop + t:pop + dam + sire | family | 1 | 64.82 | < 0.001 |
|  | t + pop + t:pop + family + sire | dam | 1 | 60.90 | < 0.001 |
|  | t + pop + t:pop + family + dam | sire | 1 | 8.59 | 0.003 |
| Finland | **t + pop + t:pop + family + dam + sire** |  |  |  |  |
|  | pop + family + dam + sire | t | 3 | 6,976.53 | < 0.001 |
|  | t + family + dam + sire | pop | 1 | 727.92 | < 0.001 |
|  | t + pop + family + dam + sire | t:pop | 3 | 157.91 | < 0.001 |
|  | t + pop + t:pop + dam + sire | family | 1 | 8.25 | 0.004 |
|  | t + pop + t:pop + family + sire | dam | 1 | 36.19 | < 0.001 |
|  | t + pop + t:pop + family + dam | sire | 1 | 6.03 | 0.014 |
| Incubation Period (ADD) | Great Lakes | **t + pop + t:pop + family + dam + sire** |  |  |  |  |
|  | pop + family + dam + sire | t | 3 | 14,370.19 | < 0.001 |
|  | t + family + dam + sire | pop | 1 | 3,495.26 | < 0.001 |
|  | t + pop + family + dam + sire | t:pop | 3 | 160.60 | < 0.001 |
|  | t + pop + t:pop + dam + sire | family | 1 | 61.35 | < 0.001 |
|  | t + pop + t:pop + family + sire | dam | 1 | 60.90 | < 0.001 |
|  | t + pop + t:pop + family + dam | sire | 1 | 14.08 | < 0.001 |
| Finland | **t + pop + t:pop + family + dam + sire** |  |  |  |  |
|  | pop + family + dam + sire | t | 3 | 2,811.03 | < 0.001 |
|  | t + family + dam + sire | pop | 1 | 706.17 | < 0.001 |
|  | t + pop + family + dam + sire | t:pop | 3 | 440.18 | < 0.001 |
|  | t + pop + t:pop + dam + sire | family | 1 | 10.58 | 0.001 |
|  | t + pop + t:pop + family + sire | dam | 1 | 36.87 | < 0.001 |
|  | t + pop + t:pop + family + dam | sire | 1 | 5.01 | 0.025 |

Table 4. Likelihood ratio test output for each model selected for length-at-hatch (mm) and yolk-sac volume (mm3) from the Great Lakes region (GLR; Lake Superior cisco (*Coregonus artedi*) and Lake Ontario cisco) and Finland region (FIR; Lake Konnevesi vendace (*C. albula*) and European whitefish (*C. lavaretus*)). The full model that was selected is bolded for each trait and region.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Trait | Region | Model | Effect Tested | df | χ2 | p-value |
| Length-at-Hatch | Great Lakes | **t + pop + dam** |  |  |  |  |
|  | pop + dam | t | 3 | 592.28 | < 0.001 |
|  | t + dam | pop | 1 | 443.20 | < 0.001 |
|  | t + pop | dam | 1 | 87.81 | < 0.001 |
| Finland | **t + pop + t:pop + family + dam** |  |  |  |  |
|  | pop + family + dam | t | 3 | 308.13 | < 0.001 |
|  | t + family + dam | pop | 1 | 1846.10 | < 0.001 |
|  | t + pop + family + dam | t:pop | 3 | 8.85 | 0.031 |
|  | t + pop + t:pop + dam | family | 1 | 15.81 | < 0.001 |
|  | t + pop + t:pop + family | dam | 1 | 41.46 | < 0.001 |
| Yolk-sac Volume | Great Lakes | **t + pop + t:pop + dam** |  |  |  |  |
|  | pop+ dam | t | 3 | 731.20 | < 0.001 |
|  | t + dam | pop | 1 | 100.48 | < 0.001 |
|  | t + pop + dam | t:pop | 3 | 36.50 | < 0.001 |
|  | t + pop + t:pop | dam | 1 | 299.71 | < 0.001 |
| Finland | **t + pop + t:pop + dam + sire + block** |  |  |  |  |
|  | pop + dam + sire + block | t | 3 | 6,976.53 | < 0.001 |
|  | t + dam + sire + block | pop | 1 | 727.92 | < 0.001 |
|  | t + pop + dam + sire + block | t:pop | 3 | 157.91 | < 0.001 |
|  | t + pop + t:pop + sire + block | dam | 1 | 82.19 | < 0.001 |
|  | t + pop + t:pop + dam + block | sire | 1 | 5.35 | 0.021 |
|  | t + pop + t:pop + sire + dam | block | 1 | 14.80 | < 0.001 |

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 | 135 |
| 4.4 | 0.00 ± 0.04 | 0.27 ± 0.10 | 125 |
| 6.9 | 0.00 ± 0.42 | 0.37 ± 0.19 | 55 |
| 8.9 | 0.00 ± 0.44 | 0.42 ± 0.12 | 54 |
|  | 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 | 191 |
| 8.9 | 0.00 ± 0.18 | 0.00 ± 0.20 | 164 |
| 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 | 135 |
| 4.4 | 0.00 ± 0.11 | 0.39 ± 0.09 | 125 |
| 6.9 | 0.00 ± 0.04 | 0.44 ± 0.09 | 55 |
| 8.9 | 0.00 ± 0.03 | 0.04 ± 0.07 | 54 |
| 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 | 191 |
| 8.9 | 0.00 ± 0.14 | 0.32 ± 0.09 | 164 |

**FIGURES:**

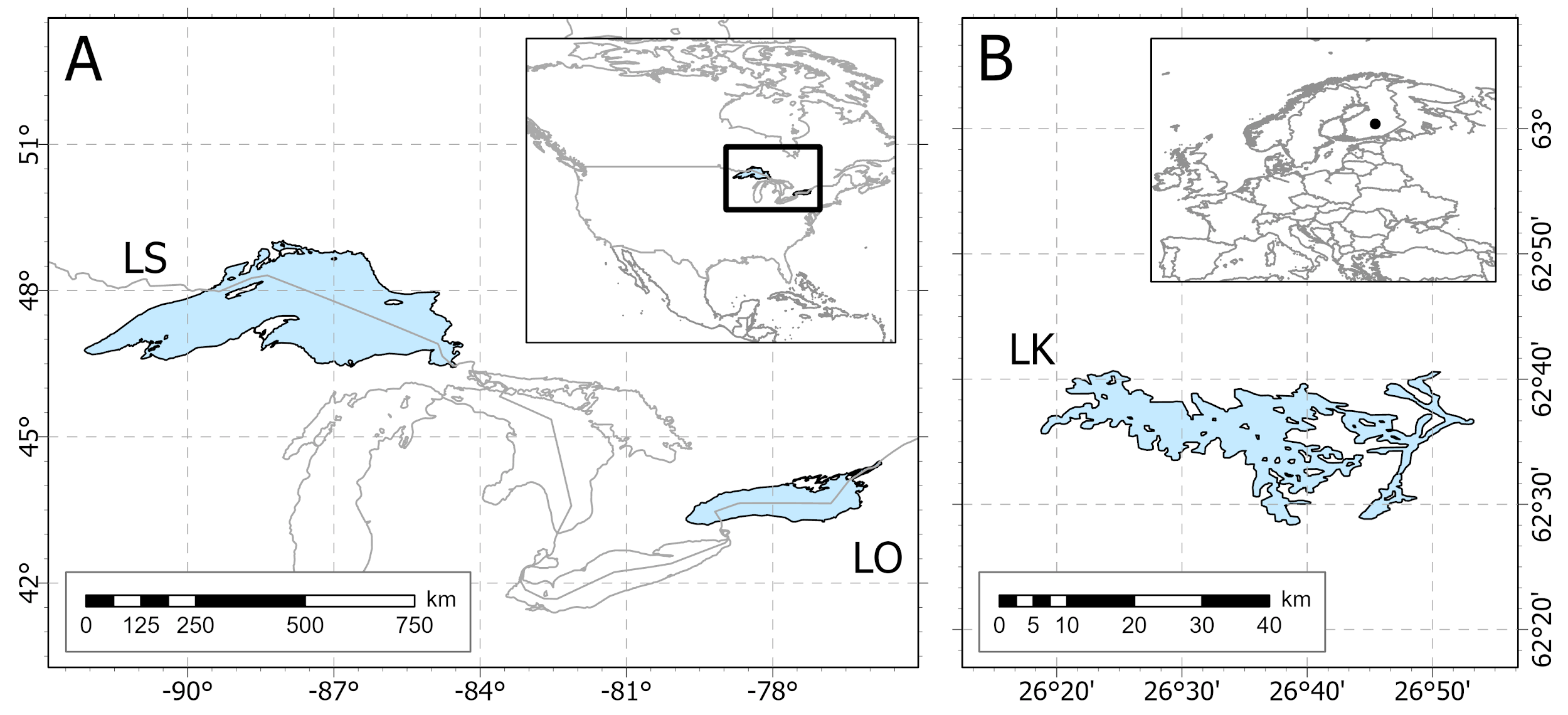


Figure 1. Map showing the location of each lake (LS = Lake Superior; LO = Lake Ontario; LK = Lake Konnevesi) sampled in North America (A) and Europe (B).

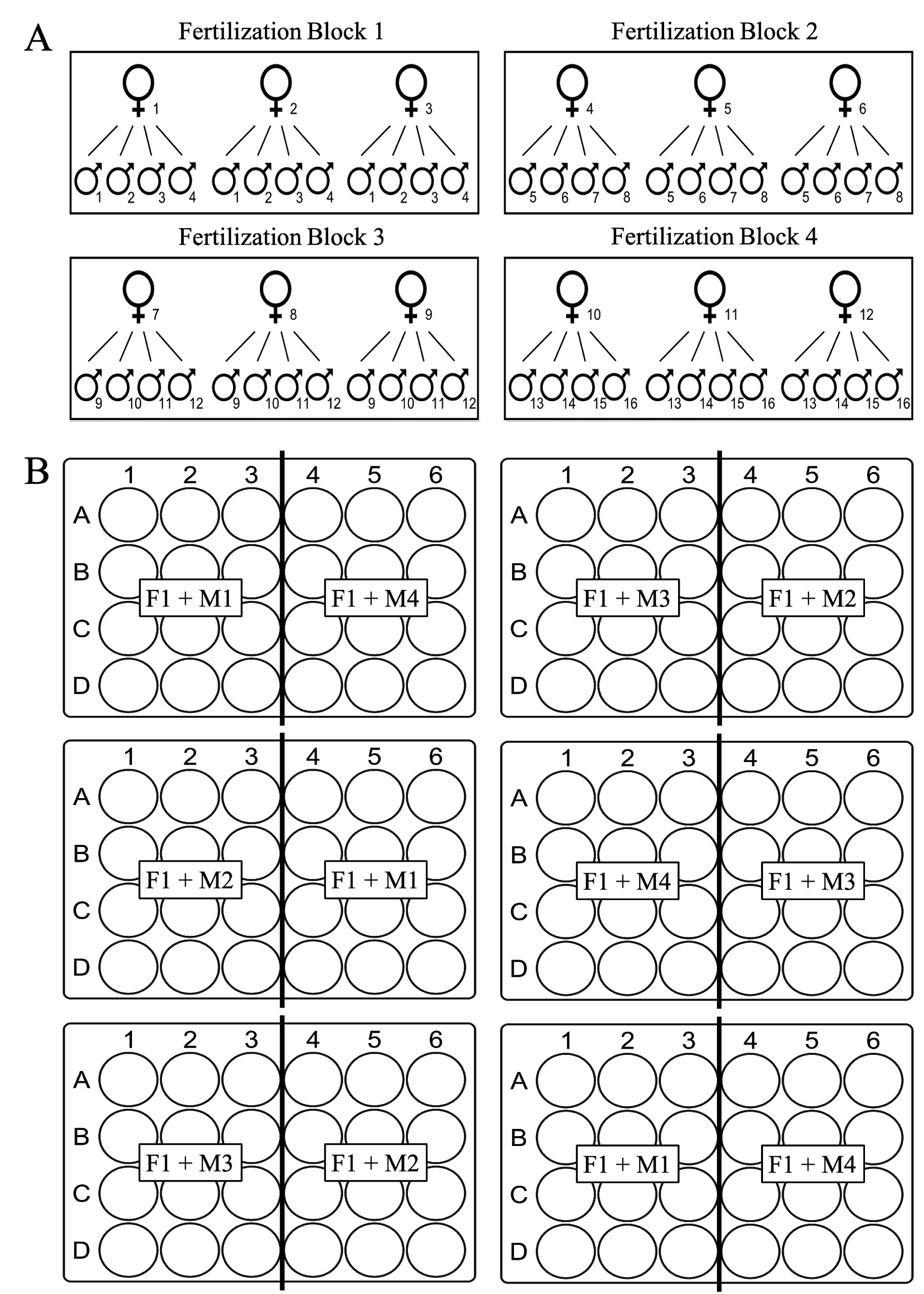


Figure 2. Crossbreeding design (A) and a theoretical division of families from a single female into microplates (B) when the number of offspring equals 36.

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 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.

Chart

Description automatically generated

Figure 4. Mean length-at-hatch (LAH) and yolk-sac volume (YSV) at each incubation temperature 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.