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

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

1Department of Biology, University of Vermont, USA

2University of Jyväskylä, Finland

3UMR CARRTEL INRA-Université Savoie Mont Blanc, France

4UMR ESE Agrocampus Ouest-INRA, France

5Rubenstein Ecosystem Science Laboratory, University of Vermont, USA

**ABSTRACT:**

Will write later.

**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 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). 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).

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 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 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. 2008b, 2008a, Vonlanthen et al. 2009, 2012, 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).

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). As ectotherms, fishes at high-latitudes experience low water temperatures overall and shorter growing seasons and exhibit lower standard metabolic rates, growth rates, and smaller size-at-age than individuals at lower latitudes (Reist et al. 2006). For stenothermic fishes, the water temperatures throughout the water column at lower latitudes may be unsuitable 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, this results in a wide range of future possibilities in how populations may respond to increasing temperatures across latitudes (Reist et al. 2006). Large-scale experimental evolution studies may aid in understanding the adaptive thermal capacity of coregonines from different latitudes and what level of adaptive response is needed to mitigate the effects of changing local 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 variables, such as water temperature.

One of the challenges in comparing population performance is the choice of offspring trait to examine fitness. The range of offspring traits are broad (*e.g.,* genetic, physiological, behavioral, etc.) and vary greatly in ease and cost to attain. Early life-history and morphological traits are often measured because of convenience, but many of those traits can be influenced through genetic and maternal effects on the gametes (Green 2008, Langley et al. 2020). 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). The environment can act directly on the spawning adults and have transgenerational effects. For example, increases in water temperature can impact the sperm of European whitefish (*Coregonus lavaretus*), shape offspring phenotype, and negatively impact post-hatching performance (Kekäläinen et al. 2018). 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. Sparse knowledge of coregonine genetic and physiological architectures of thermal plasticity limits our ability to predict coregonines resilience to the rapid rate of climate and projected increases in their thermal habitat.

We hypothesized that coregonine populations across latitudes differentially respond to warming winter conditions. Evolutionary differences in life-history traits of embryos and morphological traits of larvae to varying climates may drive thermal resilience during embryonic and larval stages. 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. To test both hypotheses, we experimentally analyzed the reaction norms of early-life stage coregonines, from known breeding crosses, across a broad latitudinal gradient to changing winter thermal regimes.

**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 (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 = 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. Post-hoc pairwise comparisons on significant fixed effects were performed with the emmeans package (Lenth 2020). 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, 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.

**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). 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 was negatively related to latitude and differed between regions (*i.e.,* continents) and among species (Table 2).

Life-history and Morphological Traits

All results for the traits, except LAH from GLR, had significant interaction effects between population and incubation temperature for both lake regions (maximum *P* = 0.031), and thus precluded any interpretation of main effects (Tables 3 and 4). Below we describe the interaction effects for each trait. All statistical results can be found in Tables 3 and 4.

*Embryo Survival (ES)*

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 3). The greatest decrease in ES between the coldest and warmest treatments was in LO-Cisco, our southernmost population (Figure 3). However, all populations, except LK-Whitefish, saw arguably high ES across all temperature treatments.

*Incubation Period (DPF)*

The effect of population depended on temperature because the differences in DPF among populations was 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 (DPF) compared to lower-latitude populations (*i.e.,* LS-Cisco and LO-Cisco) across all temperatures (Figure 3).

*Incubation Period (ADD)*

The effect of population depended on temperature because the differences in ADD among populations was 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 (ADD) 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 ADD; 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 LAH as temperature increased. 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 populations. All pairwise population and temperature comparisons for both GLR populations 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 (Figure 4). 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 (Figure 3).

*Yolk-sac Volume*

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). The difference in YSV between GLR populations decreased as temperature increased (Figure 4). YSV diverged between the two GLR populations as temperature decreased. YSV in LK-Whitefish had a similar trend but to a greater magnitude than found in GLR populations (Figure 4).

The size of spawning vendace from Lake Konnevesi were smaller than other populations and the females had smaller eggs in general. This difference in the size of spawning adults and smaller eggs eliminates our ability to compare vendace YSV and LAH results to all other populations.

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 all populations and YSV in FIR populations (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 , LAH, and YSV 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 (Table 6). The relative importance of the maternal variance was examined and explained a moderate portion of the phenotypic variance. 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). Overall, we found low levels of heritability but higher levels of maternal effects for ES, LAH, and YSV; three traits highly correlated to egg size (Tables 5 and 6). However, incubation period (both DPF and ADD) 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 in high-latitude populations. Second, YSV had a strong response to temperature among populations across latitudes and was negatively correlated with LAH. Lastly, differential levels of parental effects were found 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 ES, showed some form of latitudinal gradient to incubation temperature and suggest that coregonines are thermally adaptable. The lack of variation in ES 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, Lake Ontario, our southernmost population, did have the strongest negative response to temperature suggesting that embryo survival in southern 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 subjectively 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. Poor-feeding or metabolically costly environments may not allow for adults to efficiently support gametogenesis, especially oogenesis in females (McBride et al. 2015). In this context, our results on embryo incubation period in response to temperature 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. 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 of 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.

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 or fitness high (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. Further work examining reproductive plasticity of adults is needed but our results suggest that embryos are adapted to local incubation periods and would not possess the plasticity to synchronize development time with rising water temperatures. 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 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.,* LAH and YSV) 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 DPF and ADD; however, YSV had a stronger response to temperature among populations across latitudes compared to LAH. The trade-off between LAH and YSV is clearly 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. LAH and YSV are negatively correlated and can have large implications on larval survival. Conserving yolk-sac during development extends endogenous feeding and delays starvation after hatching. However, species with long incubation periods often are fully developed before hatching and require yolk to sustain basal metabolic demands (Pavlov 1986, Falk‐Petersen and Hansen 2001). 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 trait (Lucke et al. 2020). 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.

Traits of eleuthero-embryos 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 genetic effects (*i.e.,* heritability) control a portion of early-stage offspring trait performance in coregonines. Larger and older females typically produce higher quality eggs and therefore higher quality offspring (Roff 1994, Stewart 2011, Hixon et al. 2014). 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. Incorporating an individual-based approach to conservation and restoration efforts can help manage for individuals that may possess the ability to modulate their thermal response to compensate for at least part of the environmental effects imposed by changing water temperatures. Maintaining these short-term plastic responses within populations may render coregonines more resilient to temperature changes.

Latitudinal Compensation

An additional explanation of latitudinal variation could be a form of latitudinal compensation in various metabolic processes (Conover and Schultz 1995). 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 response also raises questions concerning possible causal mechanisms. Molecular 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

Within freshwater lakes, water temperature is fundamental for 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 phenotypes through developmental 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 lengths (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 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:**

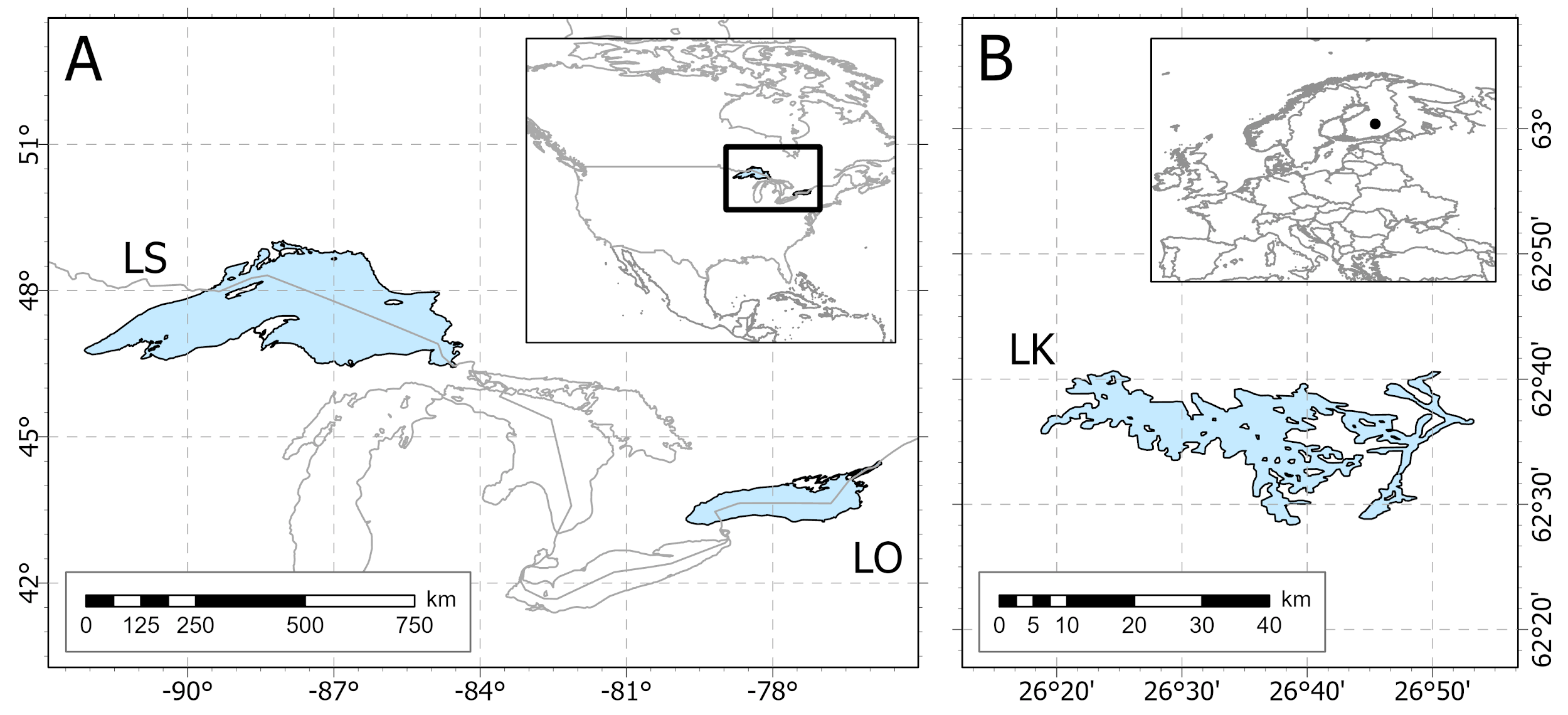


Figure 1. Map showing the location of each lake (LS = Lake Superior; LO = Lake Ontario; LK = Lake Konnevesi) sampled in North America (A) and Europe (B).

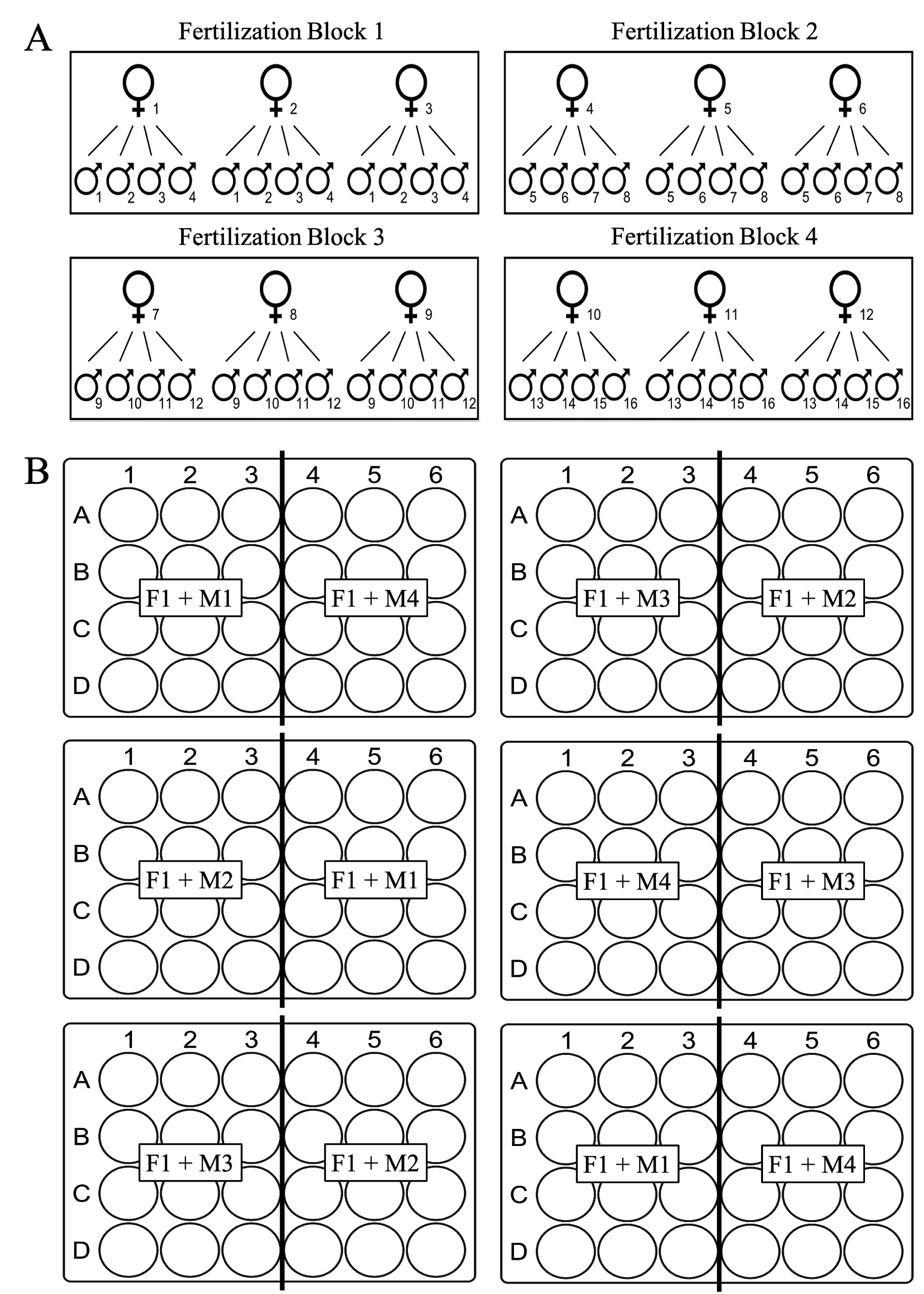


Figure 2. Crossbreeding design (A) and a theoretical division of families from a single female into microplates (B) when the number of offspring equals 36.

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.