Influence of warming temperatures on coregonine embryogenesis at local to global scales

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

1Department of Biology, University of Vermont, USA

2University of Jyväskylä, Finland

3UMR CARRTEL INRAE-Université Savoie Mont Blanc, France

4UMR ESE Agrocampus Ouest-INRAE, France

5Rubenstein Ecosystem Science Laboratory, University of Vermont, USA

**ABSTRACT:**

Will write after feedback.

**INTRODUCTION:**

Freshwater lakes are one of the most sensitive ecosystems to climate change (Woolway et al. 2020). One of the greatest threats of climate change to lakes is the unprecedented rise of water temperatures on a global scale (Austin and Colman 2007, O’Reilly et al. 2015, Woolway et al. 2017), although the rise is not projected to be consistent 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).

Warming spring water temperatures and increases in the length of the frost-free season can prolong annual growing seasons with warmer summers, longer autumns, and shorter ice-cover duration (Meehl et al. 2007). Temperature is an abiotic master factor for aquatic ecosystems because water temperature directly affects the physical and chemical properties of water, and phenological and reproductive events, metabolic rates, growth, and survival of aquatic organisms (Brett 1979, Gillooly et al. 2002, Brown et al. 2004, Ohlberger et al. 2007, Busch et al. 2012, Little et al. 2020). 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). These pressures present challenges for biodiversity conservation and sustainability of ecosystem services. To navigate challenges, a foundational understanding of the primary threats to aquatic ecosystems and organisms across a range of spatial scales from local to global is needed (Vörösmarty et al. 2010, Halpern et al. 2015, Langhans et al. 2019).

The effects of increasing temperature on lake fishes are predicted to lead to declines in cold-water species and increases in warm-water species (Comte et al. 2013, Hansen et al. 2017). Species that possess narrow optimal thermal ranges, live near their thermal limits, or have long development times at cold temperatures are at-risk under warming climate scenarios as temperature can have strong effects at early-life stages (Blaxter 1991, Pepin 1991, Ficke et al. 2007, Lim et al. 2017, Dahlke et al. 2020). Unlike their marine counterparts, most freshwater fishes are restricted to lake systems, where their ability to evade the effects of climate change is impeded due to the isolated nature of lakes (Ficke et al. 2007). Fundamental questions for eco-evolutionary and conservation biologists in a global change context include how lake fishes will respond to rising water temperatures and what adaptive mechanisms may be involved (Hairston et al. 2005, Kinnison and Hairston 2007, Pelletier et al. 2009). Shifts in physiology of lake fish populations living close to their upper thermal limits will be required if species are to persist under increasingly stressful thermal conditions (Woolsey et al. 2015, Howells et al. 2016).

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

Coregonines generally spawn during late-autumn, embryos incubate over winter, and hatch in late-spring (Karjalainen et al. 2000, Stockwell et al. 2009). The time between fertilization and hatching is inversely related to water temperature (Colby and Brooke 1970, 1973, Luczynski and Kirklewska 1984, Pauly and Pullin 1988, Karjalainen et al. 2016a). Rising spring water temperatures trigger hatching in autumn-spawned coregonine embryos (Häkkinen et al. 2002, Urpanen et al. 2005, Karjalainen et al. 2015). The length of the newly-hatched larvae is positively and negatively correlated with the length and temperature of incubation, respectively (Colby and Brooke 1970, 1973, Luczynski et al. 1984, Karjalainen et al. 2015). The long period between spawning and hatching exposes coregonines to a variety of thermal conditions, potentially resulting in a wide range of environmentally-induced phenotypes or plastic responses (Karjalainen et al. 2015, 2016a, 2016b). Some coregonines have demonstrated the ability to respond to winter temperature changes within the limits of phenotypic plasticity and through genetic adaptive changes, such as different embryo developmental rates under short and long winter conditions (Karjalainen et al. 2015, 2016a).

Geographic variation is also important to consider with phenotypic plasticity. Many fishes in high-latitudes are adapted to relatively colder waters, extensive periods of ice cover, and decreased daylight (Reist et al. 2006). Thus, in high-latitude environments, populations can show differential long-term adaptation to climates across a latitudinal gradient (Conover and Present 1990, Yamahira and Conover 2002, Chavarie et al. 2010, Wilder et al. 2020). For example, a number of fishes have demonstrated an inverse relationship between length of the growing season and reproductive characteristics (*i.e.,* countergradient variation; Conover 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). Fishes at high latitudes experience lower temperatures overall and shorter growing seasons and should exhibit lower standard metabolic rates, growth rates, and smaller size-at-age than individuals at low latitudes (Reist et al. 2006). However, for cold-water stenothermic fishes, water temperatures at low latitudes may exceed their optimal range for significant portions of the growing season, or the amount of optimal thermal habitat narrow, while water temperatures at high latitudes may remain near the optimum for maximal growth efficiency throughout the growing season (Conover and Schultz 1995). Because water temperature has a great influence on fish physiology and can vary across latitudes, a wide range of responses by populations to increasing temperatures across latitudes is possible (Reist et al. 2006). Coregonines occur broadly across northern latitudes and are an ideal group to test how cold-water fishes may adapt to climate-driven shifts in environmental variables, such as water temperature. Large-scale experimental studies may aid in understanding the adaptive thermal capacity of fishes from different latitudes and what level of adaptive response is needed to mitigate the effects of changing local environments (Hoffmann and Sgrò 2011).

Our objective was to experimentally analyze the response of early-life stage coregonines, within conspecifics across lake systems, between congeners within the same lake system, and among congeners across all lake systems, to a thermal gradient using a novel incubation method that enables global comparisons. We hypothesized that coregonines would have differential levels of phenotypic plasticity in life-history and morphological traits of embryos in response to warming winter incubation conditions based on their locally adapted environments. We predicted coregonines that share the same thermal environment respond similarly and geographically distinct groups with different thermal environments respond dissimilarly to increasing incubation temperatures. Alternatively, coregonines adapted to lower incubation water temperatures and longer winters have more efficient physiological processes and higher flexibility in development rates, compared to coregonines living at warmer water temperatures and in locations with short winters.

**METHODS:**

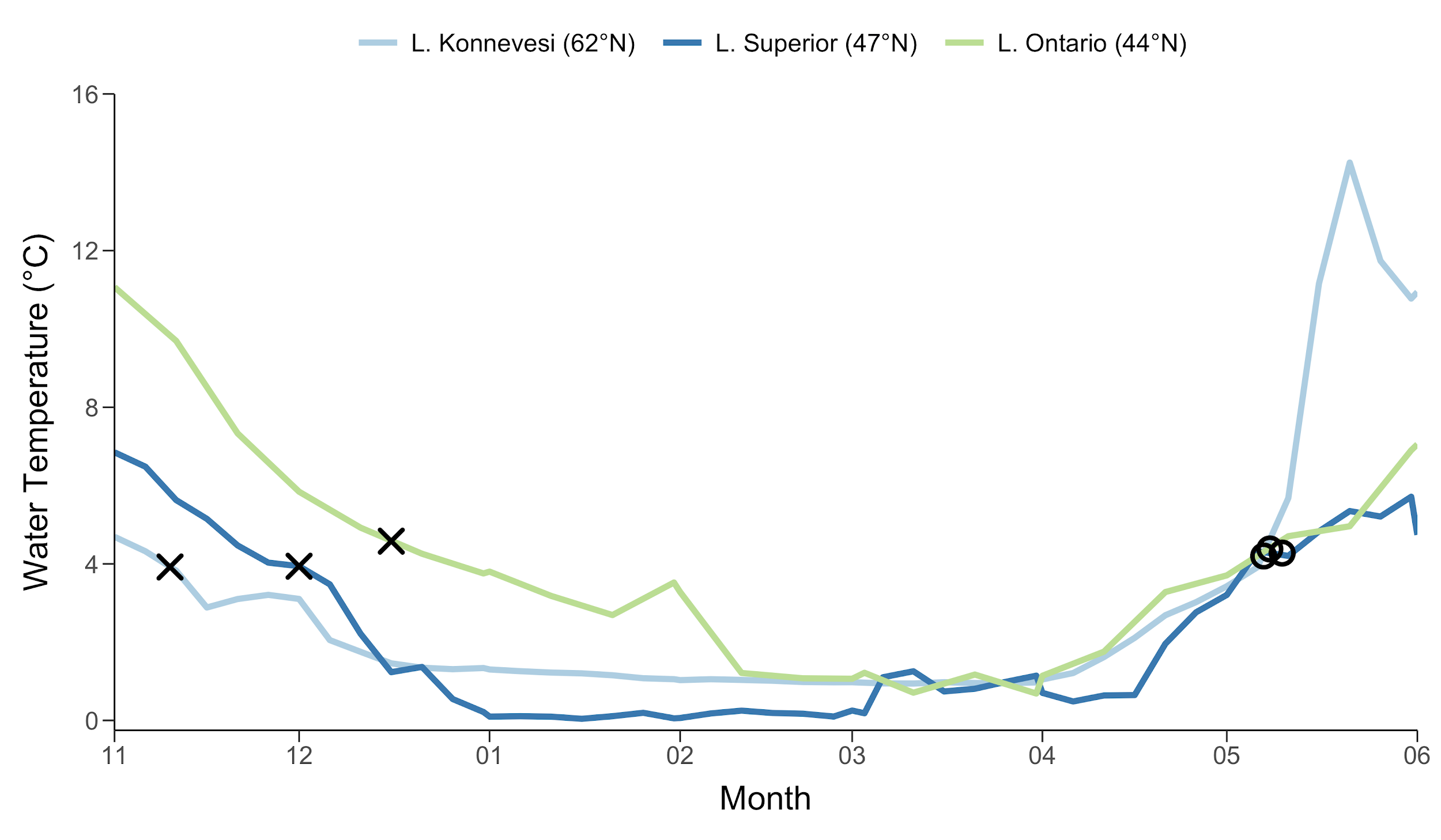
Study Species and Locations

We used a cross-lake, cross-continent, cross-species approach to evaluate the responses and thermal tolerances of coregonine embryos to changing thermal regimes. Wild-caught populations of cisco (*Coregonus artedi*) in Lake Superior (LS-Cisco; USA/Canada) and Lake Ontario (LO-Cisco; USA/Canada), and vendace (*C. albula*; LK-Vendace) and European whitefish (*C. lavaretus*; LK-Whitefish) in Lake Southern Konnevesi (Finland; Figure 1) were sampled.

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

Vendace (*C. albula)*

European whitefish (*C. lavaretus)*



Adult Collections

Adults were sampled using gillnets in Lake Superior, trap nets in Lake Ontario, and seines in Lake Southern Konnevesi. Adult field collections occurred during coregonine spawning periods for Lake Ontario and Lake Superior. On Lake Southern Konnevesi, adults were collected prior to spawning and held in aquaculture pools with water fed directly from the lake until spawning was initiated. All sampling, fertilization, and experimental work for study groups on each continent were conducted at a single laboratory in North America (University of Vermont (UVM), USA) and Europe (University of Jyväskylä (JYU), Finland). Experiments were performed during the 2018-19 season in Finland and the 2019-20 season in the USA.

For clarity, our operational use of a study group is to represent a single species within a single lake (*e.g.,* cisco in Lake Superior).

Crossing Design and Fertilization

Eggs and milt were stripped from dams and sires from each study group 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 group. The crossing design maximized 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. Adults used in the experiment were divided 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 with an equal amount of milt (5-15 μl) 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 with water 2-3 times until the water was clear. Reconstructed fresh water was used during fertilizations (OECD ISO 6341:2012) to standardize the chemical properties of the water used among study groups and between labs. Embryos were transported in coolers either by shipping overnight for Lake Superior or driven same-day for Lake Ontario. A temperature logger recorded air temperature inside the cooler during transport (Lake Superior: mean (SD) = 2.80°C (0.21); Lake Ontario: mean (SD) = 3.28°C (0.37)). No embryo transport was required for Lake Southern Konnevesi. Demographic data (*e.g.,* total length, mass, and egg diameter) 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.

Rearing Conditions

Embryos from successfully fertilized families were individually distributed into 24-well cell culture microplates and incubated in 2 ml of reconstructed fresh water. Reconstructed fresh water was used during incubation to maintain sterility, prevent bacterial growth in the wells, and eliminate the need for fungicide treatments on the embryos. A total of 36 embryos per family were used for Lake Southern Konnevesi species and 48 embryos per family for each of Lake Ontario and Lake Superior cisco. Families were randomly distributed across three or four microplates (*i.e.,* 12 eggs per family per microplate and two families per 24-well microplate). Microplates from each study group were incubated at target constant temperatures of 2.0 (coldest), 4.5 (cold), 7.0 (warm), and 9.0°C (warmest) and randomly placed in climate-controlled chambers at UVM (Memmert® IPP260Plus) and climate-controlled rooms at JYU (Huurre®). Experimental incubation temperature treatments were chosen to mimic in situ temperatures and to exceed optimum embryonic development temperatures. Forced airflow was used in both the climate-controlled chambers and rooms to ensure equal air circulation around the microplates. All microplates were covered to minimize evaporation. Microplate orientation and position were rotated weekly to eliminate any temperature heterogeneity within the chambers and rooms. 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 (< XX mins?) maintenance periods. Microplates were checked weekly for dead eggs and the eye-up stage. During the hatch period, microplates were checked on a two-day cycle for newly hatched larvae. All newly hatched larvae were photographed for life-history and morphological traits. For Lake Southern Konnevesi, the larvae were preserved in ethanol at hatch and flushed and soak in distilled water for 15 min before measuring the total length and fresh mass under the microscope (Karjalainen 1992).

Water temperature during incubations were maintained near the target incubation temperature for the cold and warm treatments at each lab. Incubation water temperatures for the cold and warmest treatments were lower than the target incubation temperature at JYU, but not at UVM (Table 1).

Life-History and Morphological Traits

Embryo survival was estimated as the percent of embryos surviving between the eye-up and hatch stages. Incubation period was assessed by two variables: the number of days from fertilization to hatching (days post-fertilization; DPF) and the sum of the degree-days (accumulated degree-days; ADD). Total length-at-hatch (mm) and yolk-sac volume (YSV; mm3) were measured from five individuals per family at, or as close as possible to, 50% hatching for each family. Yolk-sac volume was calculated assuming the shape of an ellipse (Blaxter 1963):

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

Statistical Analyses and Estimation of Variance Components

Embryo survival was analyzed as a binomial response variable, and incubation period, length-at-hatch, and yolk-sac volume at hatching as continuous response variables. Early embryo mortality induced from fertilization failure produced inequalities in the number of offspring among families and an unbalanced design. The sample size for incubation period is a function of embryo survival and subsequently resulted in an unbalanced design. Therefore, binary data (*i.e.,* embryo survival) were analyzed with binomial generalized linear mixed-effects models (LMM) and normally distributed data (*i.e.,* incubation period, length-at-hatch, and yolk-sac volume) were analyzed with restricted maximum likelihood LMMs with the lme4 package (Bates et al. 2015). To eliminate any confounding effects between continents, conspecific ciscos were analyzed independently from congeners in Lake Southern Konnevesi, resulting in two models: Great Lakes (Lake Superior and Lake Ontario) cisco and Lake Southern Konnevesi vendace and European whitefish. Population (for cisco only), species (for Lake Southern Konnevesi only), 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 or species, depending on the continent, and incubation temperature effects in addition to individual parental effects (dam, sire, and family 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, species, incubation temperature, interaction effects, and any random-effects selected were determined using a likelihood ratio test between the maximal model and reduced models with the model effect of interest removed.

To allow for interspecific comparisons, the response to temperature for each trait was standardized to the optimal temperature for each study group. The coldest incubation temperature treatment (2.0°C and 2.2°C; Table 1) was assumed to be the optimal incubation temperature. For each trait, the within-family mean was calculated for each temperature treatment and the percent change from the optimal temperature estimated. Standard error was calculated as the among-family variation in percent change.

The phenotypic variance components were partitioned into random effects for dam, sire, dam:sire interaction, and random residual variance components using mixed-effects models with the fullfact package (Houde and Pitcher 2019) for each study group and incubation temperature treatment. Negative variance components were treated as zero (Neff and Pitcher 2005). The percent of total phenotypic variation was used to calculate the correlation between each variance component and the increase in incubation temperature for each study group. European whitefish from Lake Southern Konnevesi were removed from this analysis due to a low embryo survival and a low number of families.

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

**RESULTS:**

Spawning Adults

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

The LK-Vendace females had the smallest egg diameters and LO-Cisco females had the largest egg diameters among the study groups (Table 3). LK-Whitefish and LS-Cisco egg diameters were similar (Table 3).

Life-History and Morphological Traits and Variance Components

All cisco traits, except LAH, had significant interaction effects between population and incubation temperature (maximum *P* < 0.001; Tables 4 and 5). All vendace and European whitefish traits had significant interaction effects between species and incubation temperature (maximum *P* = 0.031; Tables 4 and 5). The interaction effects precluded any interpretation of main effects, but did suggest contrasting norms of reaction for the model groups. Below we describe the interaction effects and the temperature and population pairwise comparisons for cisco LAH. The dam effect was significant in all traits for all study groups (maximum *P* < 0.001; Tables 4 and 5). The sire effect was significant for DPF and ADD in all study groups, and LAH in vendace and European whitefish (maximum *P* = 0.025; Tables 4 and 5). The dam:sire effect was significant in all traits, except LAH in cisco and YSV, for all study groups (maximum *P* = 0.004; Tables 4 and 5). All statistical model results can be found in Tables 4 and 5.

*Embryo Survival*

Embryo survival was highest among all study groups at the coldest temperature and lowest at the warmest temperature (Figure 3). The effect of population for cisco depended on temperature because embryo survival was higher for LO-Cisco (99.3%) than LS-Cisco (80.0%) at the coldest temperature but not different between populations (<0.1%) at the warmest temperature (Figure 3). LS-Cisco and LO-Cisco embryo survival responded differently to increased incubation temperature. For Lake Southern Konnevesi, the effect of species depended on temperature because the difference in embryo survival between LK-Vendace and LK-Whitefish was less pronounced at the coldest temperature (29.0%) than at the warmest temperature (50.5%; Figure 3). LK-Vendace and LK-Whitefish embryo survival had a differential temperature response as LK-Whitefish had a greater decrease (74.4%) than LK-Vendace (17.7%) from the coldest to warmest incubation temperatures. LK-Whitefish had the strongest, decreasing response to increasing incubation temperatures compared to all other study groups (Figure 3).

In the phenotypic variance component analysis, the residual error was the largest component of phenotypic variation in embryo survival (means >55.2%) for all study groups (Figure 4, SI Table 1). The mean dam variance had the highest percentage, excluding error, of the phenotypic variation in embryo survival for LK-Vendace (17.4%), LS-Cisco (24.1%), and LO-Cisco (19.9%; Figure 4, SI Table 1). The dam variance component correlations for embryo survival had either negative or no correlations to increasing temperature; however, sire and error variances had either positive and no correlation suggesting that as the dam component decreases at higher temperatures the importance of the sire component and environmentally-induced error increases (Table 6).

*Incubation Period (days post-fertilization)*

The number of days post-fertilization to hatching was highest for all study groups at the coldest temperature and decreased as temperature increased (Figure 3). For cisco, DPF was higher for LO-Cisco (179.2 days) than LS-Cisco (154.3 days) at the coldest temperature and the difference between populations was less pronounced at the warmest temperature (5.0 days; Figure 3).

For Lake Southern Konnevesi, the effect of species depended on temperature because the difference in DPF between LK-Vendace and LK-Whitefish was less pronounced at the coldest temperature (8.9 days) than at warmest temperature (27.3 days; Figure 3). All study groups had similar responses to temperature, with between 54.2 to 68.3% decreases in DPF from the coldest to warmest treatments. However, LS-Cisco, LO-Cisco, and LK-Whitefish had a greater decrease in DPF (66.1, 68.3, 65.3%, respectively), than LK-Vendace (54.2%; Figure 3).

In the phenotypic variance component analysis, the residual error was the largest component of phenotypic variation in DPF (means >60.8%) for LK-Vendace and LS-Cisco (Figure 4, SI Table 1). The mean dam variance was the highest percentage, including error, of the phenotypic variation in DPF for LO-Cisco (47.1%). LK-Vendace and LS-Cisco had similar mean dam variances for DPF across all temperatures, with 28.1 and 21.0%, respectively (Figure 4, SI Table 1). The DPF correlations for dam and error variances had a differential response to temperature with negative dam correlations and positive error correlations for LS-Cisco and LO-Cisco, while LK-Vendace had positive sire correlations and negative error correlations (Table 6).

*Incubation Period (accumulated degree-days)*

Accumulated degree-days were highest for all study groups at 6.9°C (Figure 3). The effect of population for cisco depended on temperature because ADD was higher for LO-Cisco (531.9 and 547.7 ADD) than LS-Cisco (461.0 and 492.5 ADD) at the cold and warm temperatures, respectively, and the differences between populations were less pronounced at the coldest and warmest temperatures (49.2 and 41.3 ADD, respectively; Figure 3). LS-Cisco and LO-Cisco ADD responded similarly to increasing incubation temperature. For Lake Southern Konnevesi, the effect of species depended on temperature because the difference in ADD between LK-Vendace and LK-Whitefish was less pronounced at the coldest temperature (7.7 ADD) than at the warm temperature (198.1 ADD; Figure 3). LK-Vendace and LK-Whitefish ADD had a differential temperature response as LK-Vendace had a greater increase (198.4%) than LK-Whitefish (159.4%) from the coldest to warm treatment. LK-Vendace had the strongest, increasing response to increasing incubation temperatures compared to all other study groups (Figure 3).

In the phenotypic variance component analysis and correlations, ADD had a similar response as DPF among all study groups as the data only had a different temperature scaling factor (Figure 4, SI Table 1, Table 6).

*Length-at-Hatch*

All study groups had a common, decreasing response in LAH as temperature increased (Figure 5). Temperature and population main effects were significant for cisco. All pairwise population and temperature comparisons for cisco were significant (maximum *P* < 0.001; Table 5). LS-Cisco and LO-Cisco responded to increasing incubation temperature with a 15.9 and 13.8% respective decrease in LAH from the coldest to warmest treatments. For Lake Southern Konnevesi, the effect of species depended on temperature because the difference in LAH between LK-Vendace and LK-Whitefish was more pronounced at the cold and warm temperatures (2.73 and 2.72 mm, respectively) than at the coldest and warmest temperatures (2.68 and 2.61 mm, respectively; Figure 5). LK-Vendace and LK-Whitefish each responded similarly to temperature with a 9.0 and 9.2% respective decrease in LAH from the coldest to warmest treatments. LS-Cisco and LO-Cisco LAH had a stronger, decreasing response to increasing incubation temperatures than LK-Vendace and LK-Whitefish (Figure 5).

In the phenotypic variance component analysis, the residual error was the largest component of phenotypic variation in LAH (means >49.2%) for all study groups (Figure 6, SI Table 1). The mean dam variance had the highest percentage, excluding error, of the phenotypic variation in LAH for LK-Vendace (40.6%), LS-Cisco (38.2%), and LO-Cisco (17.1%; Figure 6, SI Table 1). The LAH correlations for each study group had a similar response to temperature with negative or no dam correlations, negative or no sire correlations, and positive or no dam:sire correlations. All three study groups had different error correlations for LAH, with a negative, positive, and no correlations for LK-Vendace, LS-Cisco, and LO-Cisco, respectively (Table 6).

*Yolk-sac Volume*

Yolk-sac volume was highest for all study groups at 9.0°C and decreased as temperature decreased (Figure 5). For cisco, the difference in YSV was similar between populations at the warmest incubation temperature (0.04 mm3) but diverged as incubation temperature decreased; YSV in LO-Cisco (0.40 mm3) was smaller than LS-Cisco (0.64 mm3) at the coldest temperature (Figure 5). Yolk-sac volume in LS-Cisco and LO-Cisco responded differently to incubation temperature, with a 203.6 and 311.0% respective increase from the coldest to warmest treatment. For Lake Southern Konnevesi, the effect of species depended on temperature because the difference in YSV between LK-Vendace and LK-Whitefish was less pronounced at the coldest temperature (0.20 mm3) than at the warmest temperature (1.07 mm3; Figure 5). LK-Vendace and LK-Whitefish had the strongest response to temperature with an increase in YSV of 445.0 and 536.6% from the coldest to warmest treatment, respectively. LK-Vendace and LK-Whitefish had a stronger, increasing response to increasing incubation temperatures in YSV than LS-Cisco and LO-Cisco (Figure 5).

In the phenotypic variance component analysis, the residual error was the largest component of phenotypic variation in YSV (means >53.9%) for all study groups (Figure 6, SI Table 1). The mean YSV dam variance was the highest percentage, excluding error, of the phenotypic variation for LK-Vendace (23.9%), LS-Cisco (20.5%), and LO-Cisco (23.9%; Figure 6, SI Table 1). The LAH correlations for dam, dam:sire, and error variance components had differential responses to temperature with positive dam, positive dam:sire, and negative error correlations for LK-Vendace, while LS-Ciso had inverse correlations to LK-Vendace (Table 6). All LO-Cisco variance components had no correlation to temperature (Table 6).

**DISCUSSION:**

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

Embryo survival had an overall negative correlation with increasing temperature among all study groups. However, populations of ciscos and congeneric species from the same lake (*i.e.,* vendace and European whitefish) had contrasting levels of response to temperature. LK-Whitefish embryo survival had the strongest, negative response to temperature (74.4%) and all other study groups were impacted less (< 26% survival loss) by increasing temperatures. The contrasting levels of response in embryo survival to increased incubation temperatures among study groups was surprising because temperature is known to be the main force determining coregonine embryo development (Karjalainen et al. 2015) and survival (Colby and Brooke 1970, Brooke and Colby 1980, Luczynski and Kirklewska 1984). If temperature was a dominant factor for embryo survival, we would have expected similar responses among all study groups. Additionally, our experiment, temperature aside, provided near-optimal incubation conditions to individually reared embryos and these conditions are idealized compared to what occurs in the wild. For instance, embryos in the wild are deposited on the substratum and are exposed to deposited sediment that can impact survival (Müller 1992). Interaction between temperature and sediments are likely, and temperature increase may act as a catalyzer of embryo sensitivity to sediment stress (Mari et al. 2016). Even though temperature did negatively impact embryo survival in our experiment, the effect of temperature in the wild could be even stronger.

Our result that incubation periods from LK-Vendace and LK-Whitefish were longer and had a stronger responses to increasing temperatures, even at the warmest incubation temperatures, supports previous knowledge that vendace and European whitefish from Lake Southern Konnevesi have a high degree of developmental flexibility (Karjalainen et al. 2015). The contrasting response between vendace and European whitefish was likely due to species differences (Karjalainen et al. 2015) and ecotypes (*i.e.,* pelagic versus benthic), as benthic species should develop quicker than pelagic individuals (Mcphee et al. 2012). Additionally, the different magnitude of temperature responses among all congeners suggests a differential level of developmental plasticity to increasing incubation temperatures among species and locations. Long, relatively cold incubations may require a shorter period of spring warming for individuals to initiate hatching, while short, relatively warm incubations may require a longer period of warmer spring conditions to hatch (Karjalainen et al. 2015). If winter water temperatures rise as embryos incubate, the ability to match optimal spring nursery conditions may be weakened (Cushing 1990, Karjalainen et al. 2015, Myers et al. 2015). Populations that are more resilient to increasing or variable winter incubation temperatures may have a better opportunity to regulate ontogeny and control the time of hatching.

Fish spawning strategies are variable, ranging in frequency from daily to once in a lifetime and in timing from the same time each year to across all seasons (McBride et al. 2015). For many species, spawning strategies and breeding patterns are constrained by the adult body condition and the environment (Jørgensen et al. 2006, van Damme et al. 2009, Muir et al. 2014, McBride et al. 2015). In this context, the short duration of cisco embryo incubation periods when exposed to high temperatures was notable. High-latitude populations typically spawn earlier in autumn and may have the opportunity to shift timing of reproduction later into the season, while still providing an adequate incubation period for embryo development, if water temperatures continue to rise as a result of climate change. However, low-latitude coregonine populations already spawn in late-autumn (Stockwell et al. 2009, Eshenroder et al. 2016), which begs the question: do low-latitude populations have capacity to spawn later in the winter if temperatures continue to rise? Winter spawning may lead to less vulnerability to contemporary climate change. For instance, Atlantic herring (*Clupea harengus*) have both autumn- and winter-spawning stocks in the North Sea that share the same summer feeding grounds and start oocyte development at the same time (van Damme et al. 2009). Similarly, coregonines can exhibit contrasting spawning strategies.

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

Lake morphology is also important to consider for the question of a winter- or spring-spawning adaptation; deeper lakes could sufficiently provide cold thermal refuges at greater depths if suitable spawning habitat is available. Spring-spawning ciscos in Lac des Écorces, where a 4°C summer stratum does not exist, initiate spawning when spring water temperatures reach 6°C at depths ranging from 20-30 m (Hénault 1986, Hénault and Fortin 1989, 1991). This strategy of spawning in deeper, colder water allows for normal embryogenesis throughout the summer to mitigate high water temperatures during the summer period at shallow depths. Model projections of suitable thermal and oxythermal habitat for cisco indicate deeper and less eutrophic lakes will likely provide the best cold-water habitat as water temperatures and land uses change (Jacobson et al. 2010, Herb et al. 2014, Schmitt et al. 2020). While deep lakes may possess acceptable thermal refugia for coregonines, access to and requirements for suitable spawning and incubation habitat is unknown for most populations.

In addition to lower survival and shorter incubations as temperature increases, we also found both similar and contrasting responses to temperature in morphological traits (*i.e.,* length-at-hatch and yolk-sac volume) among study groups. The contrast in morphological traits among study groups and locations is likely related to different egg sizes at fertilization. Smaller eggs will produce smaller larvae, requiring a lower growth and development rate and less demand on maternal yolk than larger eggs. The demand for yolk and egg size are positively related and temperature during embryogenesis is positively related to metabolic rate (Hodson and Blunt 1986, Kamler 2008). The steady decline in YSV for LK-Vendace and LK-Whitefish as incubation temperatures decreased, but less variability in LAH across temperatures, suggests a high efficiency to convert yolk into somatic tissues across all temperatures where maximal LAH is constrained by egg size. In contrast, both cisco populations had a steady decline in YSV and increase in LAH as incubation temperatures decreased, suggesting a low yolk conversion efficiency at warmer temperatures. Regardless of the mode, our results suggest a synergistic relationship among species, location, egg size, incubation period, and incubation temperature in determining the phenotype of LAH and YSV.

The trade-off between LAH and YSV is well documented in larval fish physiology (Blaxter 1991). Climate change impacts may only exacerbate the importance of each morphological trait in determining either a match or mismatch between larval coregonines and their zooplankton prey. Using winter water temperatures collected from Lake Superior, we can show the theoretical interactions among water temperature, spawning period, incubation period, LAH, and YSV supported by our results (Figure 7). If spawning does shift to a later period from rising water temperatures, we would expect the size of eggs to increase and the fecundity of females to decrease (Figure 7). While our experiments used constant incubation temperatures due to logistical constraints, the impact different spring warming rates can have on the time of hatching and the size of larvae should not be ignored. Lake Southern Konnevesi vendace and European whitefish previously exhibited flexibility in embryo development rates and feeding windows under different warming scenarios (Karjalainen et al. 2015). Such complex responses challenges our ability to predict the downstream impacts changing autumn, winter, and spring water temperatures may have on embryo and larval phenotypic plasticity.

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

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

Additionally, interpreting the impacts of parental responses within an environmental context continues to be important to determine how parental effects may mitigate species’ responses to rapid climate change. The existence of varying parental responses raises questions concerning possible causal mechanisms. Genomic studies will be needed to better understand what is genetically impacted by increasing temperatures, how it is impacted, and when during development (*i.e.,* when is temperature most critical; Narum et al. 2013, Chen et al. 2018). A mechanistic understanding of thermal response from populations across latitudes will be essential to predict the vulnerability of species and populations to climate change.

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

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**TABLES:**

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

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

Table 2. Mean (SD) total length (TL) and fresh mass (FM) of the female and males from Lake Southern Konnevesi (LK-Vendace (*Coregonus albula*) and LK-Whitefish (*C. lavaretus*)), Lake Superior (LS-Cisco (*C. artedi*)), and Lake Ontario (LO-Cisco).

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

Table 3. Mean (SD) egg diameter of females with the number of eggs measured (N) from Lake Southern Konnevesi (LK-Vendace (*Coregonus albula*) and LK-Whitefish (*C. lavaretus*)), Lake Superior (LS-Cisco (*C. artedi*)), and Lake Ontario (LO-Cisco).

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

Table 4. Likelihood ratio test output for each model selected for embryo survival, incubation period (number of days post-fertilization; DPF), and incubation period (accumulated degree-days; ADD) from Lakes Superior and Ontario cisco (*Coregonus artedi*) and Lake Southern Konnevesi vendace (*C. albula*) and European whitefish (*C. lavaretus*). t indicates temperature, pop indicates population, and sp indicates species. The full model that was selected is bolded for each trait and species.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Trait | Species | Model | Effect Tested | df | χ2 | p-value |
| Embryo Survival | Cisco | **t + pop + t:pop + dam:sire + dam** |  |  |  |  |
|  | pop + dam:sire + dam | t | 3 | 443.54 | < 0.001 |
|  |  | t + dam:sire + dam | pop | 1 | 600.61 | < 0.001 |
|  |  | t + pop + dam:sire + dam | t:pop | 3 | 198.56 | < 0.001 |
|  |  | t + pop + t:pop + dam | dam:sire | 1 | 181.47 | < 0.001 |
|  |  | t + pop + t:pop + dam:sire | dam | 1 | 23.36 | < 0.001 |
|  | Vendace & European Whitefish | **t + sp + t:sp + dam:sire + dam** |  |  |  |  |
|  | sp + dam:sire + dam | t | 3 | 223.54 | < 0.001 |
|  | t + dam:sire + dam | sp | 1 | 993.43 | < 0.001 |
|  |  | t + sp + dam:sire + dam | t:sp | 3 | 52.94 | < 0.001 |
|  |  | t + sp + t:sp + dam | dam:sire | 1 | 1042.9 | < 0.001 |
|  |  | t + sp + t:sp + dam:sire | dam | 1 | 1015.8 | < 0.001 |
| Incubation Period (DPF) | Cisco | **t + pop + t:pop + dam:sire + dam + sire** |  |  |  |  |
|  | pop + dam:sire + dam + sire | t | 3 | 27,176.01 | < 0.001 |
|  | t + dam:sire + dam + sire | pop | 1 | 3,173.76 | < 0.001 |
|  |  | t + pop + dam:sire + dam + sire | t:pop | 3 | 1,113.95 | < 0.001 |
|  |  | t + pop + t:pop + dam + sire | dam:sire | 1 | 64.82 | < 0.001 |
|  |  | t + pop + t:pop + dam:sire + sire | dam | 1 | 60.90 | < 0.001 |
|  |  | t + pop + t:pop + dam:sire + dam | sire | 1 | 8.59 | 0.003 |
|  | Vendace & European Whitefish | **t + sp + t:sp + dam:sire + dam + sire** |  |  |  |  |
|  | sp + dam:sire + dam + sire | t | 3 | 6,976.53 | < 0.001 |
|  | t + dam:sire + dam + sire | sp | 1 | 727.92 | < 0.001 |
|  |  | t + sp + dam:sire + dam + sire | t:sp | 3 | 157.91 | < 0.001 |
|  |  | t + sp + t:sp + dam + sire | dam:sire | 1 | 8.25 | 0.004 |
|  |  | t + sp + t:sp + dam:sire + sire | dam | 1 | 36.19 | < 0.001 |
|  |  | t + sp + t:sp + dam:sire + dam | sire | 1 | 6.03 | 0.014 |
| Incubation Period (ADD) | Cisco | **t + pop + t:pop + dam:sire + dam + sire** |  |  |  |  |
|  | pop + dam:sire + dam + sire | t | 3 | 14,370.19 | < 0.001 |
|  | t + dam:sire + dam + sire | pop | 1 | 3,495.26 | < 0.001 |
|  |  | t + pop + dam:sire + dam + sire | t:pop | 3 | 160.60 | < 0.001 |
|  |  | t + pop + t:pop + dam + sire | dam:sire | 1 | 61.35 | < 0.001 |
|  |  | t + pop + t:pop + dam:sire + sire | dam | 1 | 60.90 | < 0.001 |
|  |  | t + pop + t:pop + dam:sire + dam | sire | 1 | 14.08 | < 0.001 |
|  | Vendace & European Whitefish | **t + sp + t:sp + dam:sire + dam + sire** |  |  |  |  |
|  | sp + dam:sire + dam + sire | t | 3 | 2,811.03 | < 0.001 |
|  | t + dam:sire + dam + sire | sp | 1 | 706.17 | 0.041 |
|  |  | t + sp + dam:sire + dam + sire | t:sp | 3 | 440.18 | < 0.001 |
|  |  | t + sp + t:sp + dam + sire | dam:sire | 1 | 10.58 | < 0.001 |
|  |  | t + sp + t:sp + dam:sire + sire | dam | 1 | 36.87 | < 0.001 |
|  |  | t + sp + t:sp + dam:sire + dam | sire | 1 | 5.01 | 0.025 |

Table 5. Likelihood ratio test output for each model selected for length-at-hatch (mm) and yolk-sac volume (mm3) from Lakes Superior and Ontario cisco (*Coregonus artedi*), Lake Southern Konnevesi vendace (*C. albula*), and Lake Southern Konnevesi European whitefish (*C. lavaretus*). t indicates temperature and pop indicates population. The full model that was selected is bolded for each trait and species.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Trait | Species | Model | Effect Tested | df | χ2 | p-value |
| Length-at-Hatch | Cisco | **t + pop + dam** |  |  |  |  |
|  | pop + dam | t | 3 | 894.52 | < 0.001 |
|  |  | t + dam | pop | 1 | 593.34 | < 0.001 |
|  |  | t + pop | dam | 1 | 103.91 | < 0.001 |
|  | Vendace & European Whitefish | **t + sp + t:sp + dam:sire + dam** |  |  |  |  |
|  | sp + dam:sire + dam | t | 3 | 308.13 | < 0.001 |
|  | t + dam:sire + dam | sp | 1 | 1846.10 | < 0.001 |
|  |  | t + sp + dam:sire + dam | t:sp | 3 | 8.85 | 0.031 |
|  |  | t + sp + t:sp + dam | dam:sire | 1 | 15.81 | < 0.001 |
|  |  | t + sp + t:sp + dam:sire | dam | 1 | 41.46 | < 0.001 |
| Yolk-sac Volume | Cisco | **t + pop + t:pop + dam** |  |  |  |  |
|  | pop + dam | t | 3 | 1,041.57 | < 0.001 |
|  |  | t + dam | pop | 1 | 142.63 | < 0.001 |
|  |  | t + pop + dam | t:pop | 3 | 36.46 | < 0.001 |
|  |  | t + pop + t:pop | dam | 1 | 332.96 | < 0.001 |
|  | Vendace & European Whitefish | **t + sp + t:sp + dam + sire** |  |  |  |  |
|  | sp + dam + sire | t | 3 | 918.89 | < 0.001 |
|  | t + dam + sire | sp | 1 | 795.46 | < 0.001 |
|  |  | t + sp + dam + sire | t:sp | 3 | 467.58 | < 0.001 |
|  |  | t + sp + t:sp + sire | dam | 1 | 69.88 | < 0.001 |
|  |  | t + sp + t:sp + dam | sire | 1 | 19.98 | < 0.001 |

Table 6. Phenotypic variation component correlation directions from increasing incubation temperature for embryo survival (%), incubation period (number of days post-fertilization; DPF), incubation period (accumulated degree-days; ADD), length-at-hatch (mm), and yolk-sac volume (mm3) from Lake Southern Konnevesi vendace (LK-Vendace (*Coregonus albula*)), Lake Superior cisco (LS-Cisco (*C. artedi*)), and Lake Ontario cisco (LO-Cisco). - indicates a negative correlation, + indicates a positive correlation, and 0 indicates no correlation.

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

**FIGURES:**

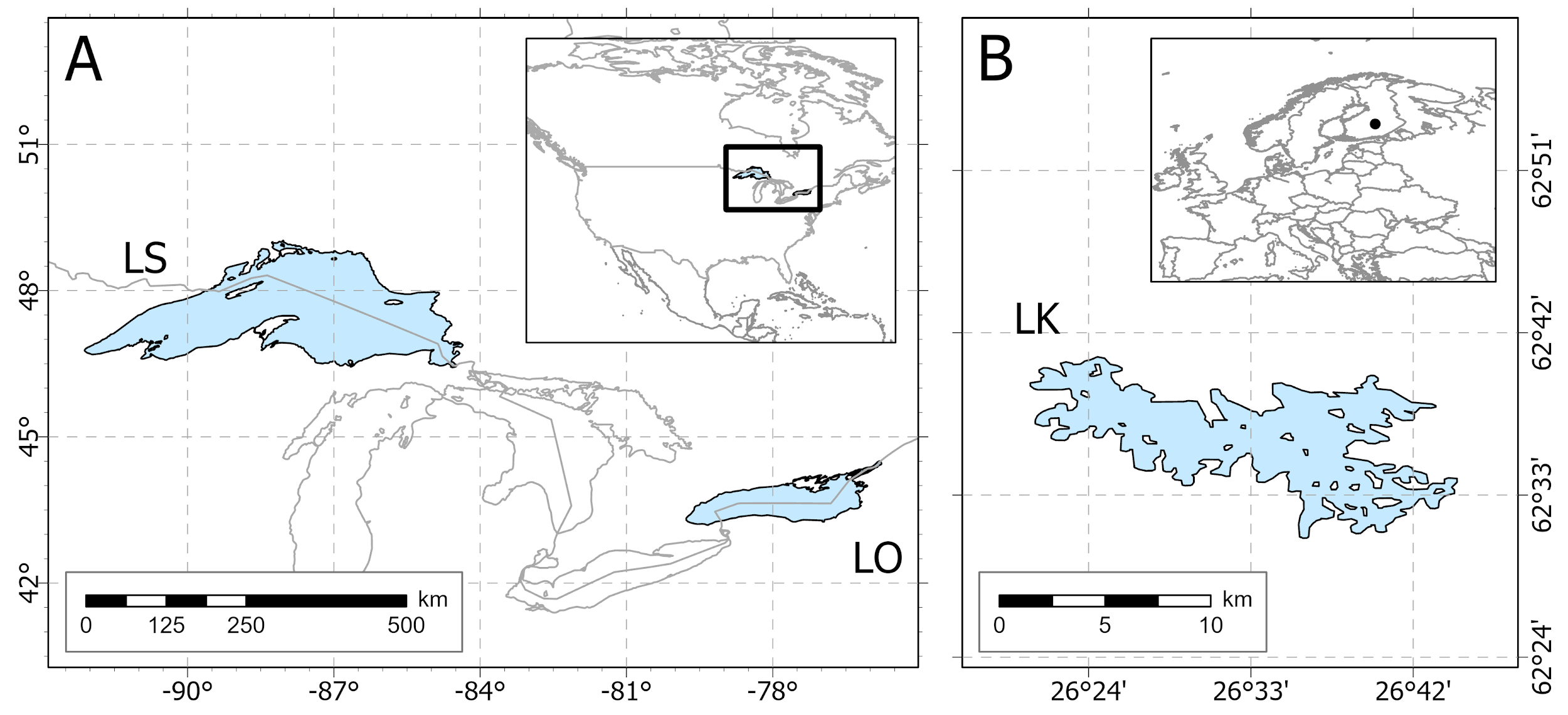


Figure 1. Map showing the location of each lake (LS = Lake Superior; LO = Lake Ontario; LK = Lake Southern Konnevesi) sampled in North America (A) and Europe (B).

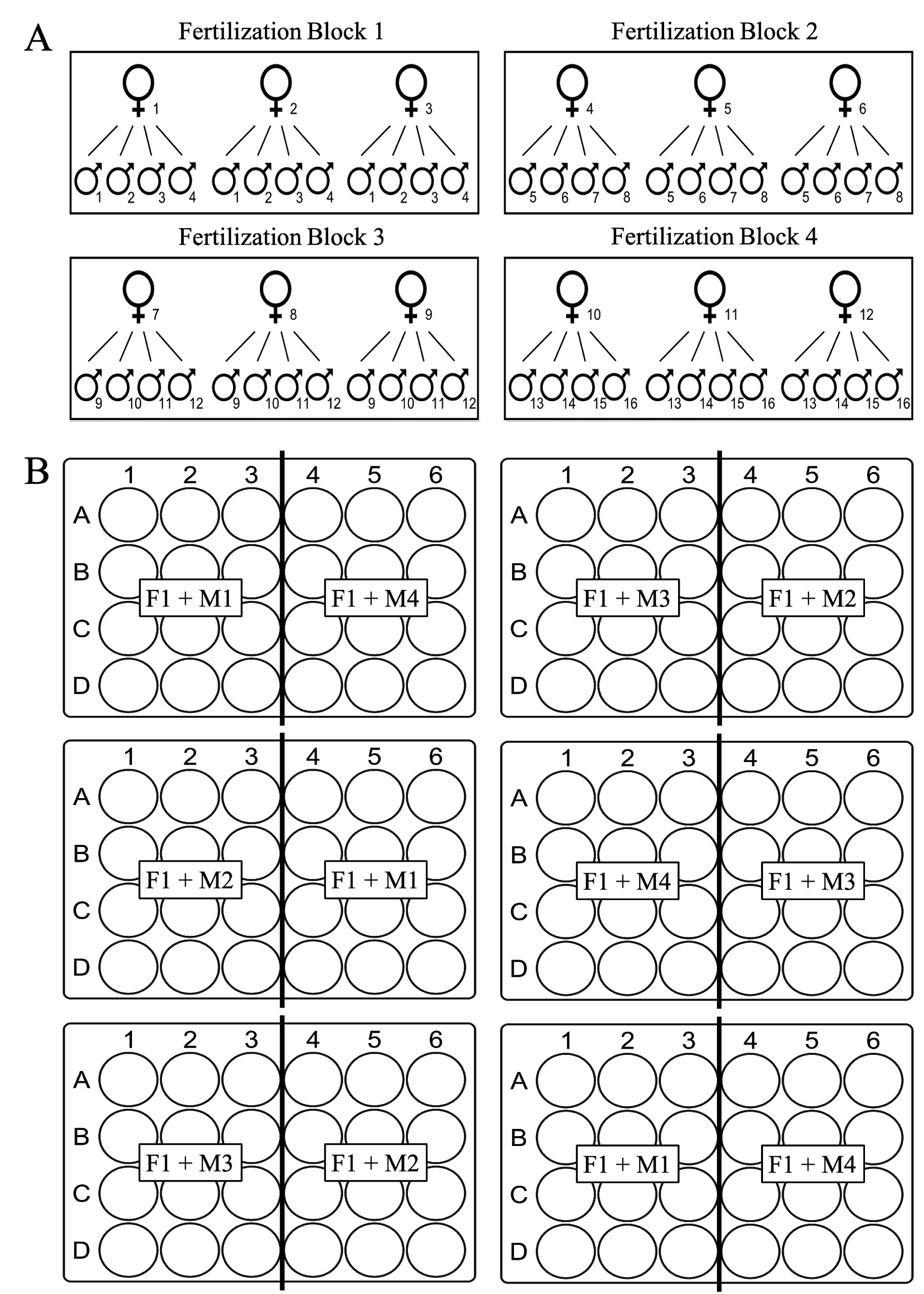


Figure 2. Crossbreeding design used for fertilizations.

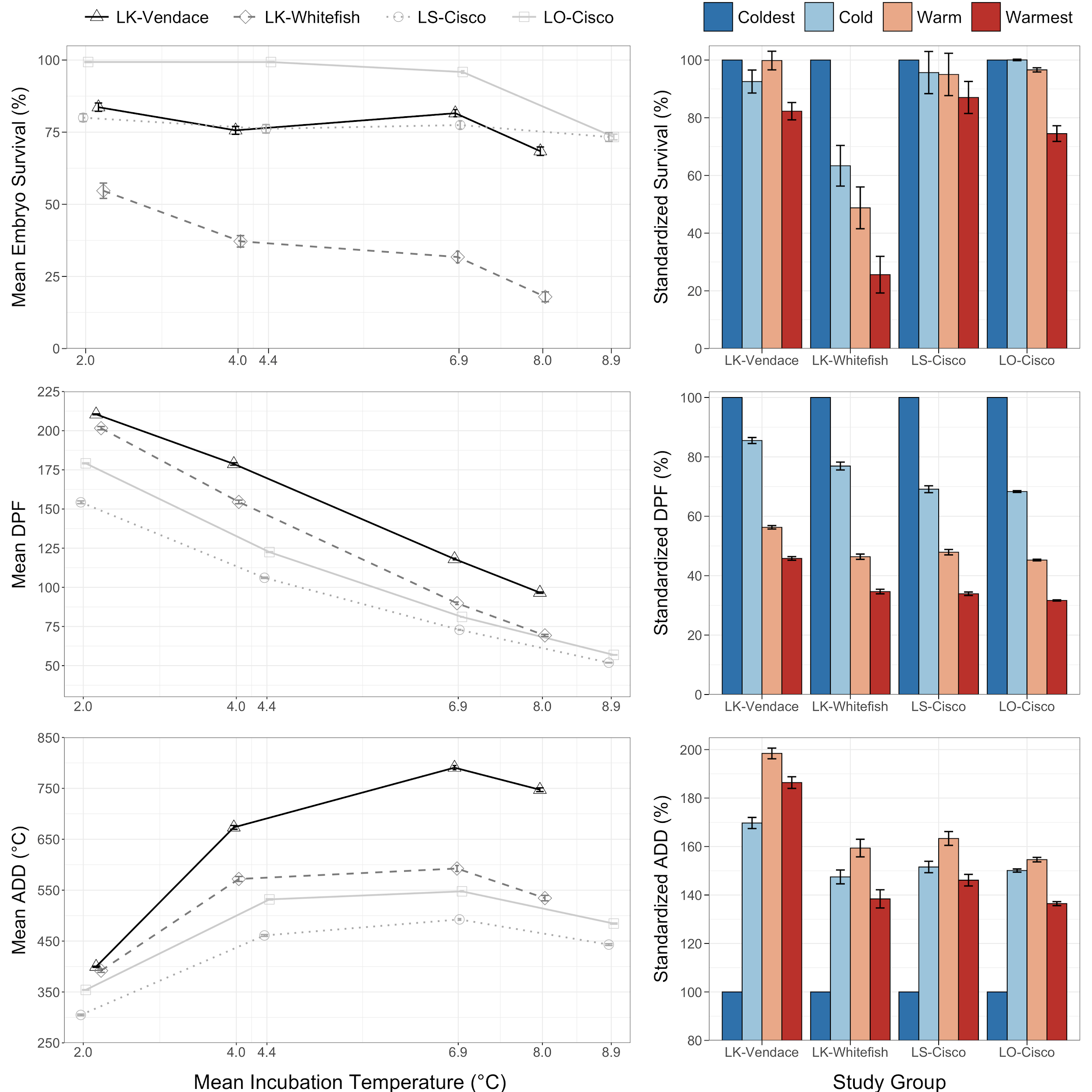


Figure 3. Mean embryo survival (%), incubation period (number of days post-fertilization; DPF), and incubation period (accumulated degree days (°C); ADD) at each incubation temperature (°C; left) and standardized temperature responses within each study group (right) from Lake Southern Konnevesi (LK-Vendace (*Coregonus albula*) and LK-Whitefish (*C. lavaretus*)), Lake Superior (LS-Cisco (*C. artedi*)), and Lake Ontario (LO-Cisco). Error bars indicate standard error.

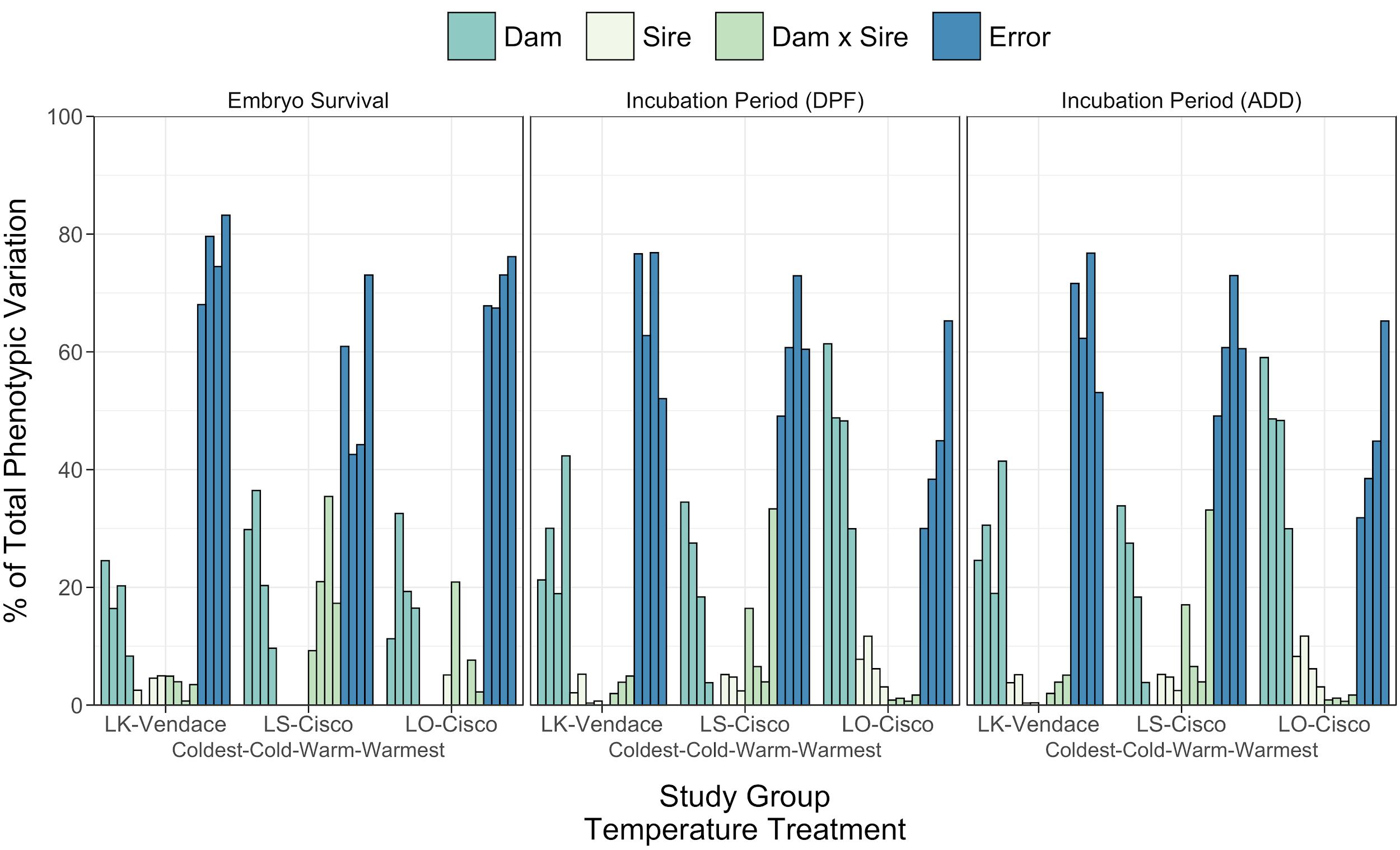


Figure 4. Percent of total phenotypic variation across temperature treatments for embryo survival, incubation period (number of days post-fertilization; DPF), and incubation period (accumulated degree days (°C); ADD) from Lake Southern Konnevesi vendace (LK-Vendace (*Coregonus albula*), Lake Superior cisco (LS-Cisco (*C. artedi*)), and Lake Ontario cisco (LO-Cisco). Error bars indicate standard deviation.

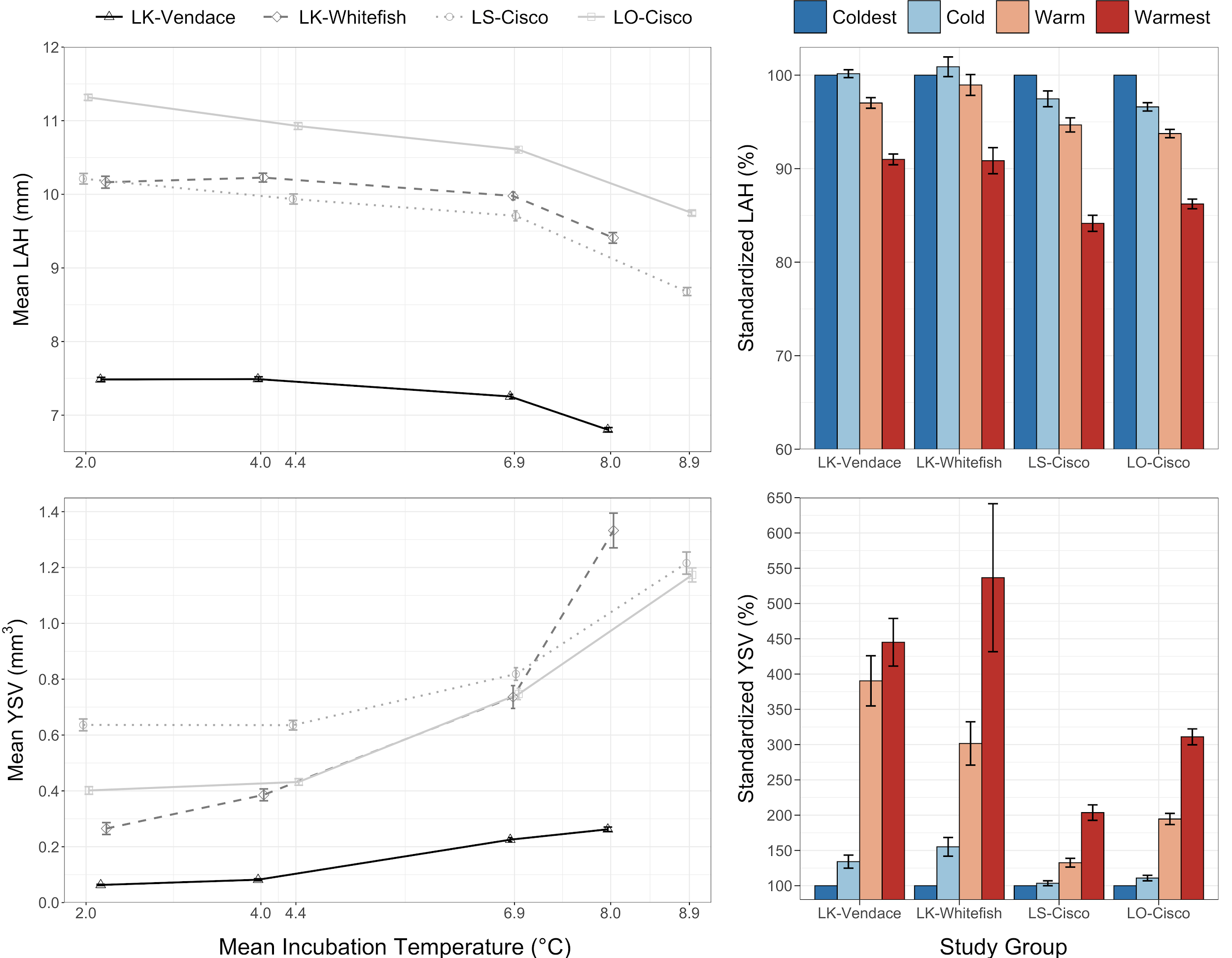


Figure 5. Mean length-at-hatch (LAH) and yolk-sac volume (YSV) at each incubation temperature (°C; left) and standardized temperature responses within each study group (right) from Lake Southern Konnevesi (LK-Vendace (*Coregonus albula*) and LK-Whitefish (*C. lavaretus*)), Lake Superior (LS-Cisco (*C. artedi*)), and Lake Ontario (LO-Cisco). Error bars indicate standard error.

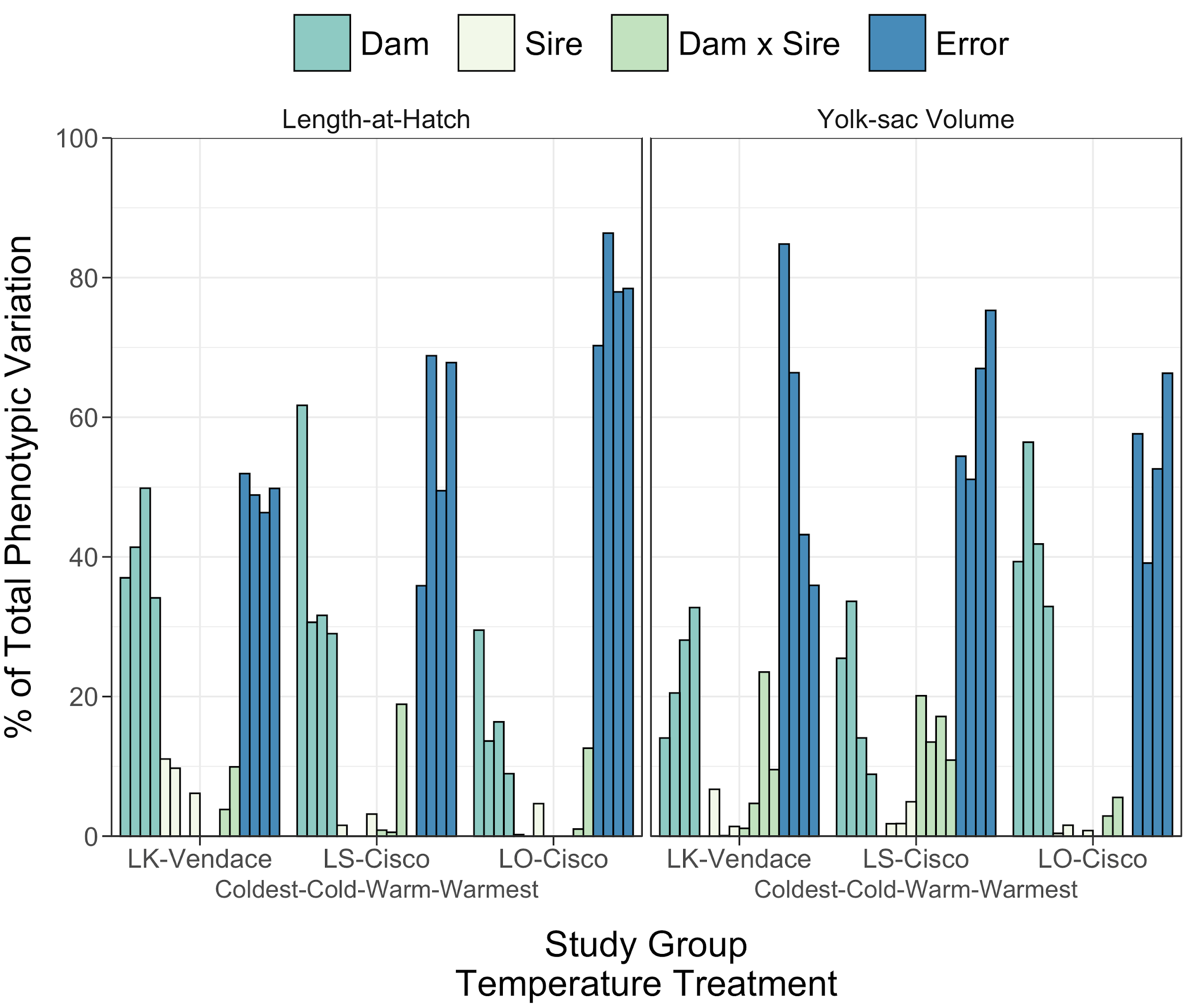


Figure 6. Mean percent of total phenotypic variation across temperature treatments for length-at-hatch and yolk-sac volume from Lake Southern Konnevesi vendace (LK-Vendace (*Coregonus albula*), Lake Superior cisco (LS-Cisco (*C. artedi*)), and Lake Ontario cisco (LO-Cisco). Error bars indicate standard deviation.

Graphical user interface, chart, line chart

Description automatically generated

Figure 7. Theoretical winter incubation periods and responses of embryo demographics under normal (2.0°C; blue) and hypothetical warm (5.0°C; orange) winter thermal regimes. The shaded regions indicate spawning periods (left) and hatching periods (right) for cisco (*Coregonus artedi*) that typically occur between 3-4°C. The 2.0°C temperature regime is water temperature data collected from Lake Superior at 10-m depth in 2018.

**APPENDIX:**

SI Table 1. Phenotypic variance component analysis for embryo survival (%), incubation period (number of days post-fertilization; DPF), and incubation period (accumulated degree-days; ADD) from Lake Southern Konnevesi vendace (LK-Vendace (*Coregonus albula*)), Lake Superior cisco (LS-Cisco (*C. artedi*)), and Lake Ontario cisco (LO-Cisco) across each incubation temperature treatment (°C).

<https://drive.google.com/file/d/1cfyAJjCw9IuF6fyL7nvYYmefiCJE8ioF/view?usp=sharing>

SI Table 2. Phenotypic variance component analysis for length-at-hatch (mm) and yolk-sac volume (mm3) from Lake Southern Konnevesi vendace (LK-Vendace (*Coregonus albula*)), Lake Superior cisco (LS-Cisco (*C. artedi*)), and Lake Ontario cisco (LO-Cisco) across each incubation temperature treatment (°C).

<https://drive.google.com/file/d/1EkgOcGoUUie4hpVH0SSJqvaVbEykUqhU/view?usp=sharing>