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RESEARCH ARTICLE | OPEN ACCESS

Winter is not coming: evaluating impacts of changing winter conditions on coregonine reproductive phenology

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Abstract – Fishes in northern latitude lakes are at risk from climate-induced warming because the seasonality in water temperature is degrading, which can change ecosystem properties and the phenology of life-history events. Temperature-dependent embryo development models were developed for a group of cold, stenothermic fishes (Salmonidae Coregoninae) to assess the potential impacts of climate-induced changes in water temperature on cisco (*Coregonus artedi*) from two populations in Lake Superior (Apostle Islands [USA] and Thunder Bay [Canada]) and one in Lake Ontario (USA), vendace (*C. albula*) in Lake Southern Konnevesi (Finland), and European whitefish (*C. lavaretus*) in lakes Southern Konnevesi, Constance (Germany), Geneva (France), and Annecy (France). Water temperatures for each study group were simulated and changes in reproductive phenology across historic (1900–2006) and three future climatic-warming scenarios (2007–2099) were investigated. Models predicted that increases in water temperatures are likely to cause delayed spawning, shorter embryo incubation durations, and earlier larval hatching. Relative changes increased as warming scenarios increased in severity and were higher for littoral as compared to pelagic populations. Our simulations demonstrated that slower cooling in the autumn and (or) more rapid warming in spring can translate into substantial changes in the reproductive phenology of coregonines among our study groups. We expect that the changes in reproductive phenology predicted by our models, in the absence of thermal or behavioral adaptation, will have negative implications for population sustainability.

Keywords: *Coregonus* / climate change / simulation modeling / reproductive phenology / water temperature

1 Introduction

Warming lake temperatures worldwide (O'Reilly *et al.*, 2015; Maberly *et al.*, 2020; Woolway, 2023) are an imminent threat to lacustrine fish (Dahlke *et al.*, 2020). Water temperature directly affects the limnological characteristics of lakes and is a master factor in regulating reproduction, development, physiology, and survival of lacustrine fishes (Gillooly *et al.*, 2002; Brown *et al.*, 2004; Cline *et al.*, 2013; Little *et al.*, 2020). Unlike riverine or marine fishes, lacustrine fish are limited in their ability to evade warming habitats. The vulnerability of fish populations varies among lakes depending on habitat connectivity, the magnitude of thermal regime change, and species and life-stage specific temperature tolerances (Dahlke *et al.*, 2020).

Holarctic fishes are predicted to be at risk because the strong seasonality in water temperature regimes in northern hemisphere lake ecosystems is degrading (Winslow *et al.*, 2017; Sharma *et al.*, 2019; Maberly *et al.*, 2020; Woolway *et al.*, 2021) and their life history is innately linked to seasonal climate patterns (Winder and Schindler, 2004). Disrupted seasonal patterns have resulted in positive feedback loops with warmer winter temperatures and (or) shorter periods of winter ice coverage, earlier and more rapid spring water warming,

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warmer and prolonged summer growing seasons and stratification periods, and delayed autumn cooling (Sharma *et al.*, 2019; Maberly *et al.*, 2020; Woolway *et al.*, 2021; Woolway, 2023). These changes in seasonal temperatures and lake mixing have modified lake ecosystem productivity (O'Reilly *et al.*, 2015; Yankova *et al.*, 2017), which can have large impacts on ecosystem structure and function (Carpenter *et al.*, 2011; Bhagowati and Ahamad, 2019).

Most observed freshwater fish responses to climate-induced changes in thermal conditions are shifts in within-lake habitat distributions (Tunney *et al.*, 2014; Guzzo *et al.*, 2017) and seasonal timing of life-history events (Parmesan, 2006; Farmer *et al.*, 2015; Slesinger *et al.*, 2021; Woods *et al.*, 2021). Spawning adults and embryos are hypothesized to be the most temperature-sensitive life-stages in fishes based on the concept of limited cardiorespiratory capacity and thermal tolerance; spawning adults need suitable thermal habitat for offspring to develop and aerobic capacity improves with cardiorespiratory development (Dahlke *et al.*, 2020). Warming waters will also shorten embryo incubation times resulting in earlier larval hatch dates (Reist *et al.*, 2006; Karjalainen *et al.*, 2015; Stewart *et al.*, 2021a). Fish reproductive strategies have generally evolved to account for seasonal changes in resources and allow for the most energy-intensive period of the consumer's reproductive phenology to align with the peak availability of prey resources (Hjort, 1914; Cushing, 1990; Lowerre-Barbieri *et al.*, 2011; Lyons *et al.*, 2015). The spatio-temporal synchrony between larval fish and their prey is believed to be an important driver of interannual variation in fish year-class strength (Cushing, 1990; Nyberg *et al.*, 2001; Straile *et al.*, 2015).

Freshwater coregonines, Salmonidae Coregoninae, are a group of cold, stenothermic fish species of high economic, ecological, and cultural importance widely distributed throughout the northern hemisphere (Bogue, 2001; Nyberg *et al.*, 2001; Zeller *et al.*, 2011; Lynch *et al.*, 2016; Hodgson *et al.*, 2020; Leppi *et al.*, 2023). Over the past several decades, many coregonine populations have declined and are the focus of reintroduction, restoration, and conservation efforts (Zimmerman and Krueger, 2009; Anneville *et al.*, 2015; Bronte *et al.*, 2017). Declines in some coregonine populations throughout their range are related to low early-life survival (Nyberg *et* al., 2001; Parks and Rypel, 2018). Reasons for declining recruitment have been linked to invasive species (*e.g.*, three-spined stickleback *Gasterosteus aculeatus* in Lake Constance) and changes in primary production (*e.g.*, re-oligotrophication in Lake Geneva) at local scales (DeWeber *et al.*, 2022; Bourinet *et al.*, 2023). However, factors influencing declining recruitment remain unknown for many bodies of water, but climate-induced increases in water temperatures during critical early-life stages may be an important driver (Nyberg *et al.*, 2001; Jeppesen *et al.*, 2012; Karjalainen *et al.*, 2015; Bourinet *et al.*, 2023).

Coregonines generally spawn near shore in late-autumn or winter (*i.e., ca.* October-January in the northern hemisphere); embryos incubate under ice or in ice-free water and hatch in late-winter or spring (Anneville *et al.*, 2007; Karjalainen *et al.*, 2015; Eshenroder *et al.*, 2016). For autumn-spawning coregonines, the seasonal decrease in water temperature initiates spawning and winter water temperature is positively related to embryo development rate and negatively related to incubation duration (Colby and Brooke, 1973; Luczyński and Kirklewska, 1984; Gillet, 1989; Karjalainen *et al.*, 2015; Eshenroder *et al.*, 2016; Stewart *et al.*, 2021a). Climate change projections suggest that warming lake temperatures in autumn and winter could alter spawning phenology, incubation time, and subsequent hatching time and survival of early-life stage coregonines (Nyberg *et al.*, 2001; Karjalainen *et al.*, 2015, 2016; Stewart *et al.*, 2021b; Vinson *et al.*, 2023).

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

2 Methods

Temperature-dependent embryo development models were developed for eight coregonine study groups, newly fit models were validated with existing *in situ* observations, lake bottom thermal regimes were developed based on climatic-warming scenarios, and future simulations for study groups were run with validated models (Fig. 1).

2.1 Study locations and species

Study groups included pelagic cisco (*Coregonus artedi*) from two populations in Lake Superior (Apostle Islands [United States of America (USA)] and Thunder Bay [Canada]) and one in Lake Ontario (USA), pelagic vendace (*C. albula)* in Lake Southern Konnevesi (Finland), and the littoral species within the European whitefish species complex (*C. lavaretus*) in lakes Southern Konnevesi, Geneva (France), and Annecy (France), and the pelagic species within the European whitefish species complex (*C. lavaretus)* in Lake Constance (Germany; Fig. 2). Study groups were selected based on the availability of water temperature, spawning, and developmental data.

Lakes Superior and Ontario are large, deep lakes (>19,000 km^2; max depths > 244 m) within the Laurentian Great Lakes system with a diverse range of trophic states, thermal conditions, and habitats. Lake Southern Konnevesi is an oligotrophic lake (120 km^2; max depth 56 m) in southern Finland with free-flowing inlet and outlet streams. Lakes

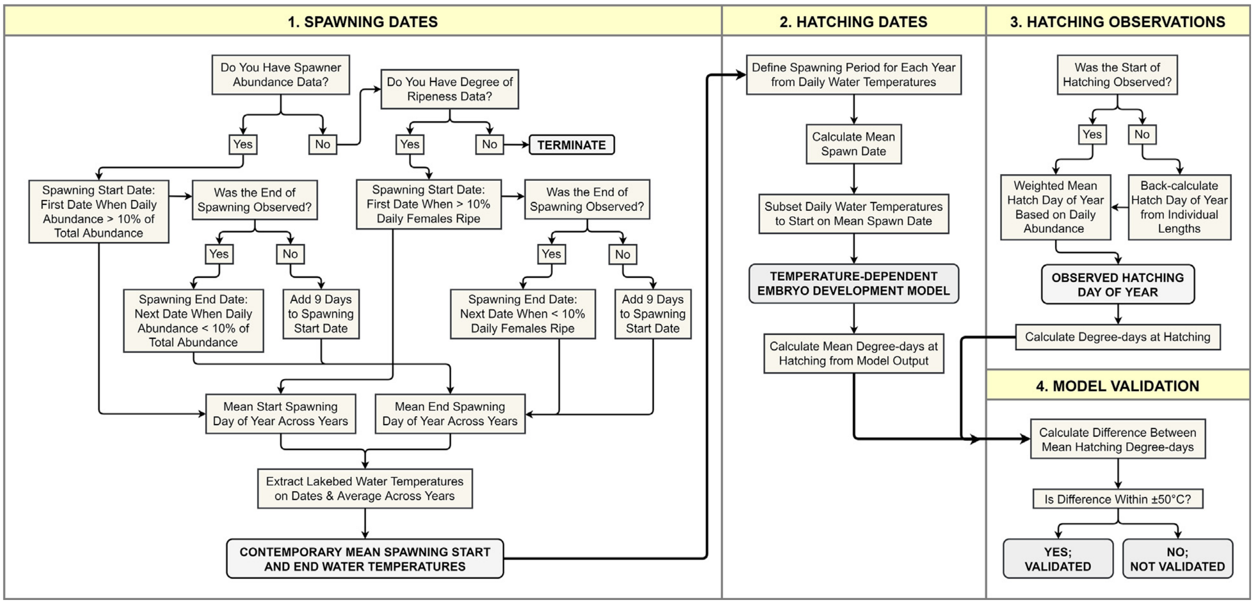

Fig. 1. Workflow diagram describing the use of *in situ* spawning, hatching, and daily lakebed water temperature data in the model validation process.

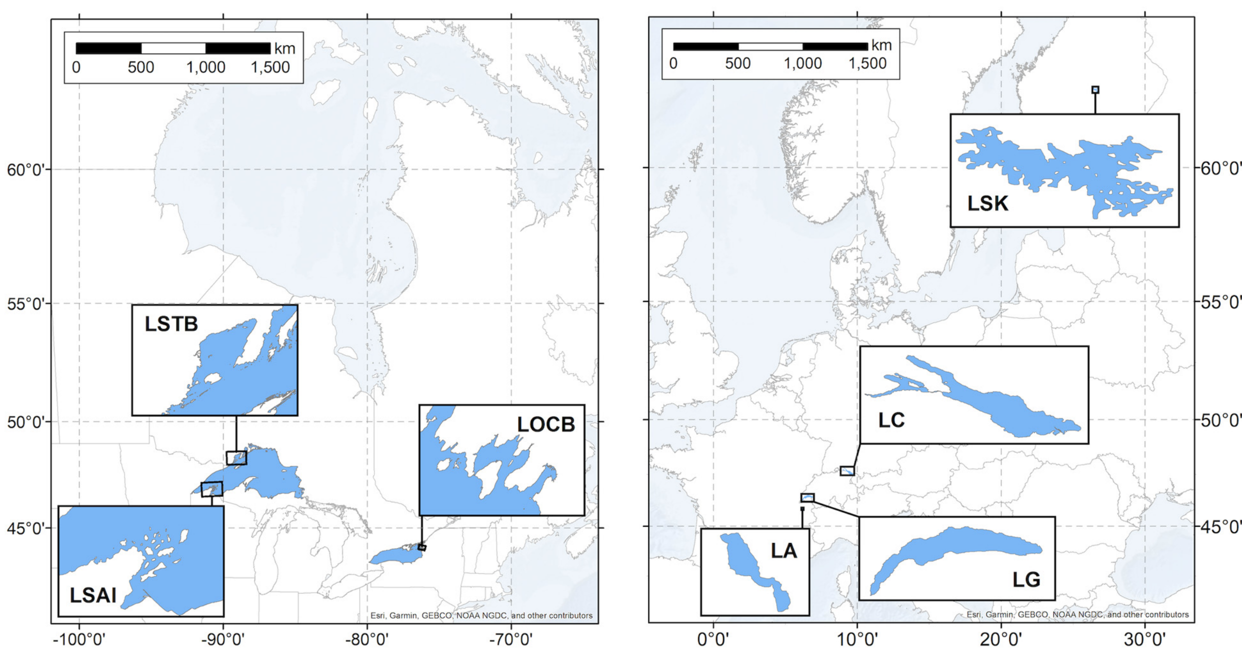

Fig. 2. Map showing the location of each study group (LSTB = Lake Superior Thunder Bay, LSAI = Lake Superior Apostle Islands; LOCB = Lake Ontario Chaumont Bay; LSK = Lake Southern Konnevesi; LC = Lake Constance; LG = Lake Geneva; LA = Lake Annecy) sampled in North America (left) and Europe (right).

Constance and Geneva are large, deep, peri-alpine lakes (>530 km^2; max depths > 250 m) in central and western Europe. Lake Annecy is a small, peri-alpine lake (28 km^2; max depth 82 m) in western Europe. Lakes Constance, Geneva, and Annecy exhibit significant thermal stratification and have been shifting towards an oligotrophic state over the last 40 years (Bourinet *et al.*, 2023).

2.2 Temperature-dependent embryo development model description

Embryo development rates were expressed as the reciprocal number of days from fertilization to a given developmental stage (Colby and Brooke, 1973; Luczyński and

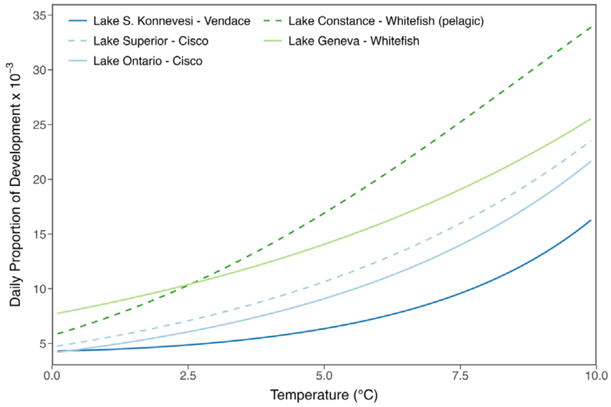

Fig. 3. Predicted daily proportion of embryo development at water temperatures (°C) from validated development to 50% hatching *(DR_{50})* models for vendace *(Coregonus albula)* from Lake Southern Konnevesi, cisco (C. *artedi*) from lakes Superior and Ontario, and European whitefish (C. *lavaretus)* from Lake Geneva, and the pelagic species of European whitefish from Lake Constance. Population-specific DR_{50} models were fit to data in Stewart *et al.*, (2021a) for *C. artedi* from lakes Superior and Ontario and *C. albula* from Lake S. Konnevesi and Stewart *et* al., in review) for European whitefish from Lake Geneva. Species-specific DR_{50} models were taken from Eckmann (1987) for *C. lavaretus* (pelagic) from Lake Constance.

Kirklewska, 1984; Eckmann, 1987). The 50% hatching development stage was chosen to be comparable among study groups. The generalized equation relating rate of development to 50% hatching (DR_{50}) with respect to incubation temperature (x; °C) is

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

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

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

DR_{50} models for cisco from lakes Superior and Ontario and vendace from Lake Southern Konnevesi were fit with experimental incubation duration data on embryos incubated at constant water temperatures of *ca.* 2.0, 4.5, 7.0, and 9.0 °C (Stewart *et al.*, 2021a; Fig. 3, Tab. 1). An additional model was fit for littoral spawning morphotypes of European whitefish from Lake Geneva using embryo incubation data. Winter temperatures at Lake Geneva in the littoral zone normally decline to only 5–7 °C, so only two incubation temperatures were evaluated (contemporary at 7.0 °C and warmer winters at 9.0 °C). Thus, only a linear model was fit for European whitefish in Lake Geneva. The semilog form (*i.e., $log_{10}DR_{50}$*) was fit to obtain model coefficients for each study group with experimental incubation data using the mean number of days from fertilization at each incubation temperature. Furthermore, published DR_{50} models were used for the littoral and pelagic spawning species of European Whitefish (*C. lavaretus macrophthalmus* and *C. lavaretus wartmanni*, respectively) from Lake Constance, vendace from Lake Kosno (Poland), and cisco from Pickerel Lake (USA; Colby and Brooke, 1973; Luczyński and Kirklewska, 1984; Eckmann, 1987; Tab. 1). Hereafter, DR_{50} models fit to each study group from experimental data (Stewart *et al.*, 2021a, in review) are referred to as population-specific models while DR_{50} models with published polynomial coefficients for species outside of our study groups (Colby and Brooke, 1973; Luczyński and Kirklewska, 1984; Eckmann, 1987) are species-specific models.

To predict development time to 50% hatching, $log_{10}DR_{50}$ was calculated for each daily mean temperature since spawning and the antilog10 taken to estimate the daily proportion of development. When the cumulative daily proportions of development equaled one, 50% hatching was assumed to have occurred.

2.3 Data sources

Fishery-dependent spawning data were available for Lake Superior (Apostle Islands and Thunder Bay; Tab. A1). Commercial fishers from Lake Superior used gillnets to target spawning aggregations and recorded date, sex, maturity, and gonad condition from a subset of their catch (*e.g.*, first 10 fish; Yule *et al.*, 2008).

Fishery-independent spawning data collected during spawning surveys or broodstock collections were available for lakes Southern Konnevesi, Annecy, Geneva, and Ontario (Tab. A1). Spawning adults were collected using gillnets for lakes Southern Konnevesi, Geneva, and Annecy and trap nets for Lake Ontario at known spawning times and locations. Spawning adults collected were either assessed for gonad condition (*i.e.*, green, ripe, spent) if actively spawning or were transported and held in hatchery ponds fed by lake water until spawning was observed. A daily distribution of spawning intensity was calculated, except for Lake Annecy where only peak spawning was reported. Daily number of ripe spawning individuals was reported for Lake Geneva, while daily gonad condition was reported for lakes Southern Konnevesi and Ontario.

Repeat larval abundance data (*i.e., ca.* weekly) were gathered for each study group to estimate dates of hatching (Tab. A1). Larval collections were made by either a seine or ichthyoplankton net through ice, or along the surface or at a stratified depth when lakes were ice-free (Perrier *et* al., 2012; Karjalainen *et al.*, 2019; Lucke *et al.*, 2020; McKenna *et al.*, 2020). All larvae collections began prior to the start of hatching or with low abundance so the date of first capture was assumed to be the start hatch date, except for the Lake Superior (Apostle Islands) study group. Larvae from Lake Superior (Apostle Islands) were sampled on fixed dates annually, presumably during or after peak hatching, and thus the hatch date of individual larvae were back-calculated from total lengths assuming an absolute growth rate of 0.18 mm day^{-1} (Oyadomari and Auer, 2007) and a length-at-hatch of 9.9 mm (Stewart *et al.*, 2021a). Daily lakebed winter water temperatures were obtained from deployed temperature loggers or sondes (*e.g.*, HOBO® Water Temperature Pro v2) for lakes Superior (Apostle Islands), Ontario, Southern Konnevesi, Geneva, and Annecy on known spawning habitat or depth (Table A.1). Only a single winter (2017-18) of lakebed temperature data was available from Chaumont Bay, Lake

Table 1. Development rate equations to 50% hatching DR_{50} for cisco (*Coregonus artedi* from lakes Superior, Ontario, and Pickerel, vendace (*C. albula)* from lakes Kosno and Southern Konnevesi, and European whitefish (*C. lavaretus*) from lakes Constance and Geneva. Population-specific DR_{50} models were fit to data for *C. artedi* from lakes Superior and Ontario, *C. albula* and *C. lavaretus* from Lake S. Konnevesi (Stewart *et al.*, 2021a), and *C. lavaretus* from Lake Geneva (Stewart *et al.*, in review). Species-specific DR_{50} models were taken for *C. artedi* from Pickerel Lake (Colby and Brooke, 1973), *C. albula* from Lake Kosno (Luczyński and Kirklewska, 1984), and *C. lavaretus* (pelagic and littoral species) from Lake Constance (Eckmann, 1987). The coefficient of determination (R^2) was provided for models fit in this paper. All coefficients are in common logarithm (log10), and coefficients from Eckmann (1987) were transformed from natural logarithm. x is the incubation temperature in °C. – indicates no value was reported.

Model group	Species	$log_{10}DR_{50}$=	R^2
Lake Superior	*C. artedi*	$-2.3289 + 0.0717x - 0.0001x^2$	0.97
Lake Ontario	*C. artedi*	$-2.3836 + 0.0643x + 0.0008x^2$	0.98
Pickerel Lake	*C. artedi*	$-2.4088 + 0.0720x + 0.0011x^2$	–
Lake Kosno	*C. albula*	$-2.3035 + 0.0651x + 0.0004x^2$	–
Lake S. Konnevesi	*C. albula*	$-2.3664 + 0.0088x + 0.0050x^2$	0.94
Lake S. Konnevesi	*C. lavaretus*	$-2.4183 + 0.0459x + 0.0032x^2$	0.96
Lake Constance	*C. lavaretus* (pelagic)	$-2.2419 + 0.1104x - 0.0033x^2$	–
Lake Constance	*C. lavaretus* (littoral)	$-2.3002 + 0.1104x - 0.0031x^2$	–
Lake Geneva	*C. lavaretus*	$-2.1159 + 0.0528x$	0.86

Ontario, and thus water temperatures from satellite surface water (https://podaac.ipl.nasa.gov/MEaSUREs-MUR) and U.S. Geological Survey Oswego River gauge (gauge number 04249000; U.S. Geological Survey, 2024) were compared to the observed lakebed winter water temperatures from Chaumont Bay in 2017-2018. The Oswego River gauge provided the closest representation of the lakebed thermal conditions of Chaumont Bay (mean daily difference = 0.77 °C) and was used as the *in situ* winter water temperatures for the Lake Ontario study group. Daily lakebed winter water temperatures for Lake Superior (Thunder Bay) were provided by the City of Thunder Bay Bare Point Water Treatment Plant, which measures water temperature at intake pipes submerged 733 m from shore at 13-m depth.

2.4 Model validation

Population-specific DR_{50} models fit from experimental incubation duration data (Stewart *et al.*, in review) were validated using *in situ* daily lakebed winter water temperatures at typical spawning depths to compare model outputs (*i.e.*, hatching dates) to the observed hatching data from eight coregonine study groups across North America and Europe. Experimental data were not available to fit population-specific models for lakes Annecy and Superior (Thunder Bay), thus the population-specific model from the closest-related study group and lake was used as the best-approximating model. Our models from Lake Geneva and the Apostle Islands in Lake Superior were therefore applied to Lake Annecy and Thunder Bay, respectively.

Initiation and completion of contemporary spawning were based on observed water temperatures (Fig. 1). Coregonine spawning data to calculate the spawning temperatures were either (1) the daily proportion of ripe females leading to spawning or (2) the daily number of spawning individuals on spawning grounds. The onset of spawning was assumed to start on the date when either >10% of females captured daily were ripe or when the number of daily spawners was >10% of the total number of spawning individuals annually. The end of spawning was calculated as the nearest date to the start of spawning when either <10% of females were ripe or when the number of daily spawners was <10% of the total number of spawning individuals annually. If the end of spawning period could not be calculated (*e.g.*, commercial roe fishery ceased once eggs were free flowing or only peak spawning was observed), the spawning period was assumed to end 9 days after the start of spawning (Straile *et al.*, 2015). The water temperatures from the first and last date of the spawning period were taken from *in situ* daily lakebed winter water temperatures and averaged across all years available to define contemporary start and ending spawning water temperatures. If the years with spawning data did not overlap the years with water temperature data, the mean starting and ending days of year for the spawning period were calculated from all years of available spawning data, and the water temperatures at each mean starting and ending spawning days of year were averaged across all available water temperature years. For Lake Constance, where the dominant species of European whitefish spawns in pelagic water and embryos sink to a depth of 200–250 m (Straile *et al.*, 2007), spawning start dates were calculated using published equations from the date that the upper 10-m of the water column reached 10 °C isothermal conditions and spawning was assumed to end after 9 days (Straile *et* al., 2015).

To validate the models for each study group, the mean spawning date was estimated from the calculated spawning start and end water temperatures for each year of available *in situ* water temperature data (Fig. 1). Mean observed hatching days of year were calculated as a weighted mean with daily larval abundance as the weight across all years available for each study group. The predicted development time to 50% hatching for each study group was calculated using daily water temperatures beginning at the mean spawning date for each population-specific model and, if applicable, the respective species-specific models from literature (Colby and Brooke, 1973; Luczyński and Kirklewska, 1984; Eckmann, 1987). The mean degree-days at hatching from all fitted models were

Table 2. Model validation results for population-specific development to 50% hatching models (DR_{50}) for cisco (*Coregonus artedi*) from lakes Superior (Apostle Island and Thunder Bay) and Ontario, vendace (*C. albula*) from Lake Southern Konnevesi, and European whitefish (*C. lavaretus*) from lakes Geneva and Annecy. Starting and ending spawning temperatures (°C) used as model parameters are listed and the model output (*i.e.*, degree-days at hatching) from population-specific and species-specific models were compared to *in situ* hatching data for each study group. N indicates the number of available years with daily *in situ* water temperatures and across which spawning temperatures were averaged. Bolded degree-days at hatching indicates the selected DR_{50} model for each study group, if one was validated. Population-specific DR_{50} models were fit to data for *C. artedi* from lakes Superior (Apostle Islands) and Ontario, *C. albula* and *C. lavaretus* from Lake S. Konnevesi (Stewart *et al.*, 2021a), and *C. lavaretus* from Lake Geneva (Stewart *et al.*, in review). Species-specific DR_{50} models were taken for *C. artedi* from Pickerel Lake (Colby and Brooke, 1973), *C. albula* from Lake Kosno (Luczyński and Kirklewska, 1984), and *C. lavaretus* (pelagic species) from Lake Constance (Eckmann, 1987).

		Mean spawning temperatures		Mean degree-days at hatching			
Study group	Species	Start	End	Observed	Pop. model	Species model	*N*
Lake Superior (Apostle Islands)	*C. artedi*	4.3	3.0	250.1	**255.7**	335.0	3
Lake Superior (Thunder Bay)	*C. artedi*	4.9	4.4	452.3	337.9	405.3	4
Lake Ontario	*C. artedi*	4.1	2.7	377.5	**359.8**	344.1	10
Lake S. Konnevesi	*C. albula*	7.4	5.6	390.7	**439.0**	269.4	3
Lake S. Konnevesi	*C. lavaretus*	6.0	4.7	292.5	395.7	200.6	3
Lake Geneva	*C. lavaretus*	8.0	6.6	792.2	374.0	332.6	26
Lake Annecy	*C. lavaretus*	7.9	6.4	342.5	370.3	**332.3**	16

estimated and compared to the mean observed degree-days at hatching for each study group. Degree-days (DD) were calculated using 0 °C as the reference temperature. A model was considered validated if the difference between the model degree-days at hatching and the mean observed degree-days at hatching was within ±50 DD. The closest validated model (*i.e.*, either the population-specific model or species-specific model) to the mean observed DD at hatching was selected for each study group.

2.5 Climate scenarios

Daily lake bottom water temperatures were simulated within the Inter-Sectoral Impact Model Intercomparison Project phase 2b (ISIMIP2b) local lake sector (Warszawski *et al.*, 2014), using the SimStrat v2.1 lake model (Gaudard *et al.*, 2019) for years 1900–2099 (Fig. A1). To drive the lake model, EWEMBI bias-corrected (Lange, 2019) climate model projections from ISIMIP2b were used, specifically projections from GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-LR, and MIROC5 for historic (1900–2006) and future periods (2007–2099) under three representative concentration pathways (RCP): RCP 2.6, 6.0, and 8.5. These pathways included a range of potential future global radiative forcing with RCP 2.6 the lowest-emission scenario and RCP 8.5 the highest-emission scenario (IPCC, 2014).

To simulate how warming water temperatures would manifest in each of our study groups, lakes from ISIMIP were used as case studies. A total of 59 modeled case-study lakes from ISIMIP were categorized into climate zones following the definitions of Maberly *et al.* (2020) and maximum depth zones of 0–10, 10–25, 25–50, and 50+ m. Water temperatures from case-study lakes were averaged across all four climate model projections by each date, climate zone, and depth category to provide a simulated daily estimate of thermal spawning habitat for each climate zone and lake depth category combination. Each study group was assigned by climate zone and typical coregonine spawning depth, and the respective simulated mean daily water temperatures were used for each study group. Only 19 of the 59 available case-study lakes matched the climate zone and depth categories of our study groups and were used (Tab. A2).

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

2.6 Model simulations

For each simulated year in the model, spawning began on the first day that the 5-day running average of simulated water temperatures dropped below the population-specific start spawning temperature and ended on the first day that the 5-day running average of simulated water temperatures dropped below the population-specific end spawning temperature. Eggs were deposited throughout the defined spawning period according to the proportional rate of daily water temperature change, where larger daily decreases in temperature resulted in higher daily spawner abundances. We modeled 500 female spawners each year, with each female depositing 100 eggs to provide a relative index of cohort size. If the simulated water temperatures did not decrease sufficiently to end spawning, spawning was assumed to end after 20 days. A spawning period of this duration is reasonable for high-latitude coregonine populations (Karjalainen and Marjomäki, 2018). Daily cohorts of deposited eggs were run through the respective validated DR_{50} model for each study group, and the hatch date was estimated.

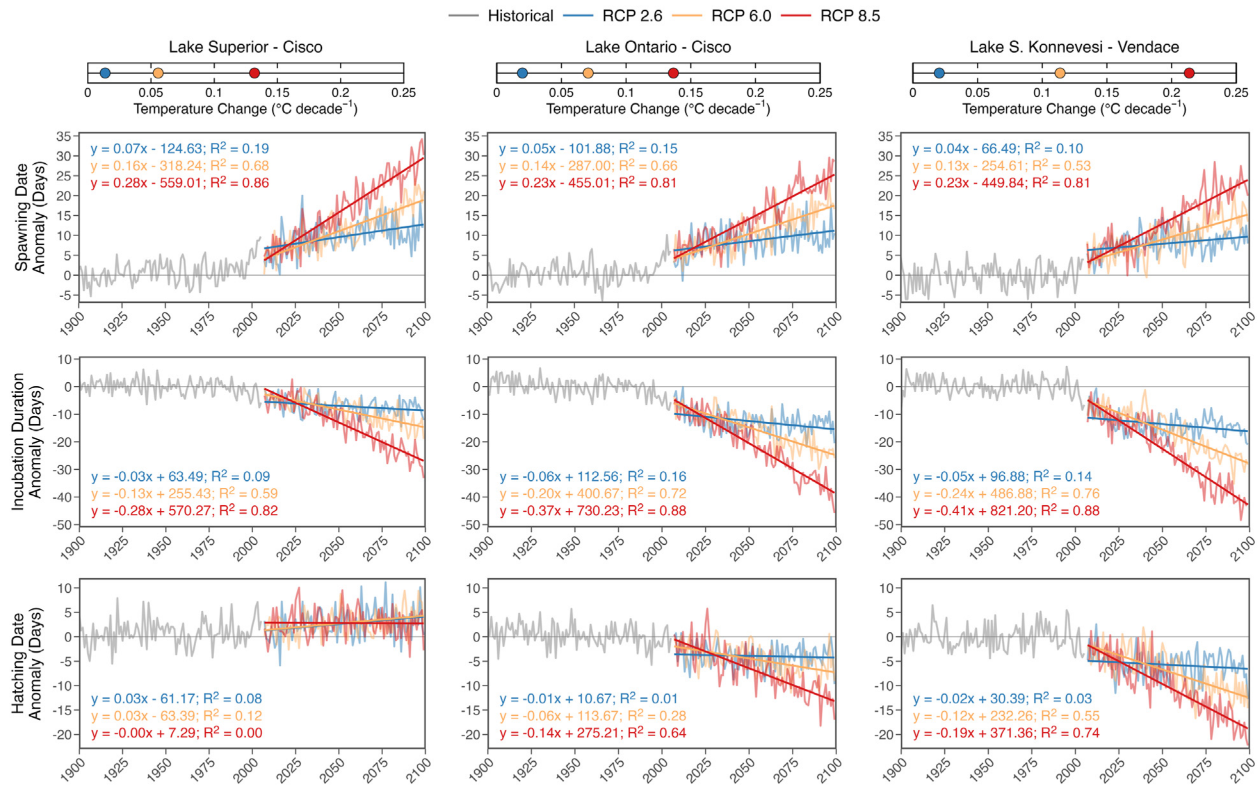

Fig. 4. Simulation model anomalies (number of days) for spawning date, incubation length, and hatching date for cisco *(Coregonus artedi)* from lakes Superior and Ontario and vendace *(C. albula)* from Lake Southern Konnevesi. Anomalies were calculated for three representative concentration pathways (RCP) from 2007–2099 compared to the mean value from the historical period (1900-2006). The rate of simulated incubation temperature (°C) change per decade is indicated in the top row for each study group and matched to the respective RCP by color. Linear regression equations for each RCP scenario and the coefficient of determination (R^2) were provided.

To estimate the magnitude of change in reproductive phenology, incubation duration was calculated for each simulated embryo and mean spawning and hatching dates for each study group across historic (1900–2005) and future periods (2006–2099). Mean spawning date, incubation duration, and hatch date anomalies were calculated as deviations from the respective mean trait value during the historical period (1900–2005) for each study group, future year, and RCP scenario. Linear regressions were fit through simulated years to trait anomalies for each study group and RCP scenario. The linear models of the trait anomalies for each RCP scenario were compared using a two-way analysis of variance (R syntax: *trait anomaly ~ year class + RCP scenario*) within each study group, and a Tukey post-hoc test was conducted if a significant difference among slopes was found (a = 0.05) using the *emmeans* package v.1.10.0 (Lenth, 2021).

All simulations and analyses were performed in R version 4.2.3 (R Core Team, 2023).

3 Results

Our population-specific models were fit, validated, and selected for cisco from lakes Superior (Apostle Islands) and Ontario, vendace from Lake Southern Konnevesi, and European whitefish from Lake Annecy (Tabs. 1 and 2). No model was validated for cisco from Lake Superior (Thunder Bay) and European whitefish from lakes Southern Konnevesi and Geneva because the difference between predicted and observed hatching was not within our confidence range (*i.e.*, ±50 DD), and thus results are not reported for these study groups (Tab. 2).

Study groups with validated DR_{50} models displayed variable development rates but were similar within species across populations (Fig. 3). DR_{50} models for European whitefish from Lake Constance had the fastest development rates while models for vendace from Lake Southern Konnevesi had the slowest development rates.

3.1 Spawning time

Model simulations predicted that spawning will be delayed for all study groups except the pelagic species of European whitefish from Lake Constance as climate change scenarios increase water temperatures (Figs. 4 and 5). The RCP 8.5 scenario resulted in the greatest deviation from the mean historical spawning time in all study groups (mean increase = 0.28 days year^{-1}).

Spawning time of European whitefish from Lake Annecy had the largest response to increased temperature (0.61 days year^{-1} at RCP 8.5), and the RCP 8.5 scenario resulted in skipped spawning years and the complete absence of adequate

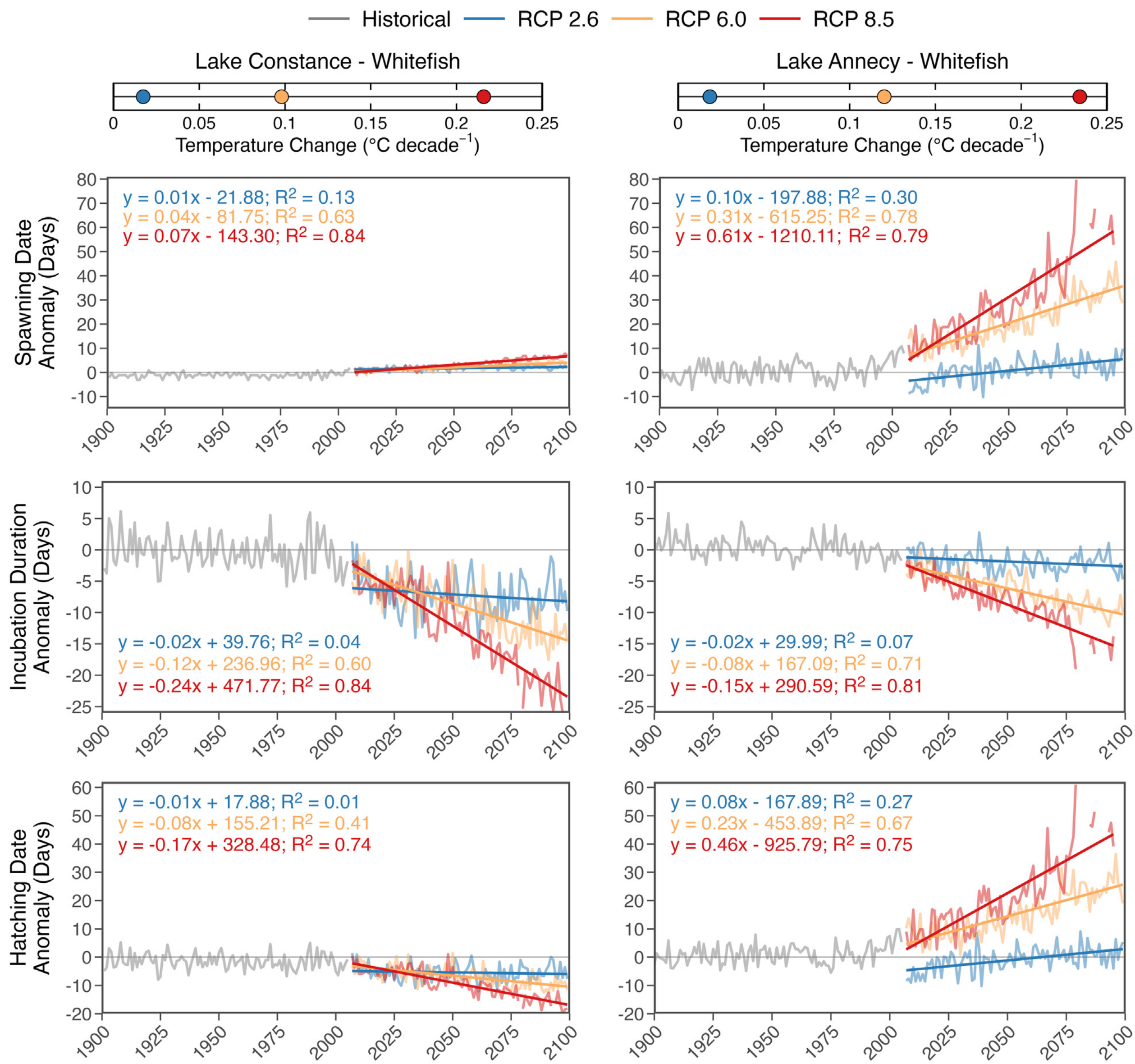

Fig. 5. Simulation model anomalies (number of days) for spawning date, incubation length, and hatching date for European whitefish *(Coregonus lavaretus)* from lakes Constance (pelagic species) and Annecy. Anomalies were calculated for three representative concentration pathways (RCP) from 2007-2099 compared to the mean value from the historical period (1900–2006). The rate of simulated incubation temperature (°C) change per decade is indicated in the top row for each study group and matched to the respective RCP by color. Linear regression equations for each RCP scenario and the coefficient of determination (R^2) were provided.

thermal habitat during the reproductive period required to initiate spawning by 2080 (Fig. 5). Cisco from lakes Superior and Ontario and vendace from Lake Southern Konnevesi had similar delayed spawning responses to increased temperatures within each RCP scenario (Fig. 4). Spawning time of European whitefish from Lake Constance responded similarly among RCP scenarios and had minimal change from historical spawning times (< 0.07 days year^{-1}; Fig. 5). All RCP anomaly slope pairwise comparisons were significantly different for spawning date within each study group ($p < 0.05$), except for vendace from Lake Southern Konnevesi between RCP 2.6 and 6.0 *(p* = 0.060; Fig. 6).

3.2 Incubation length

Embryo incubation durations (*i.e.*, number of development days) were predicted to decrease because of increased water temperatures from climate change for all study groups examined (Figs. 4 and 5). The greatest deviation in incubation length from the mean historical incubation length was the RCP

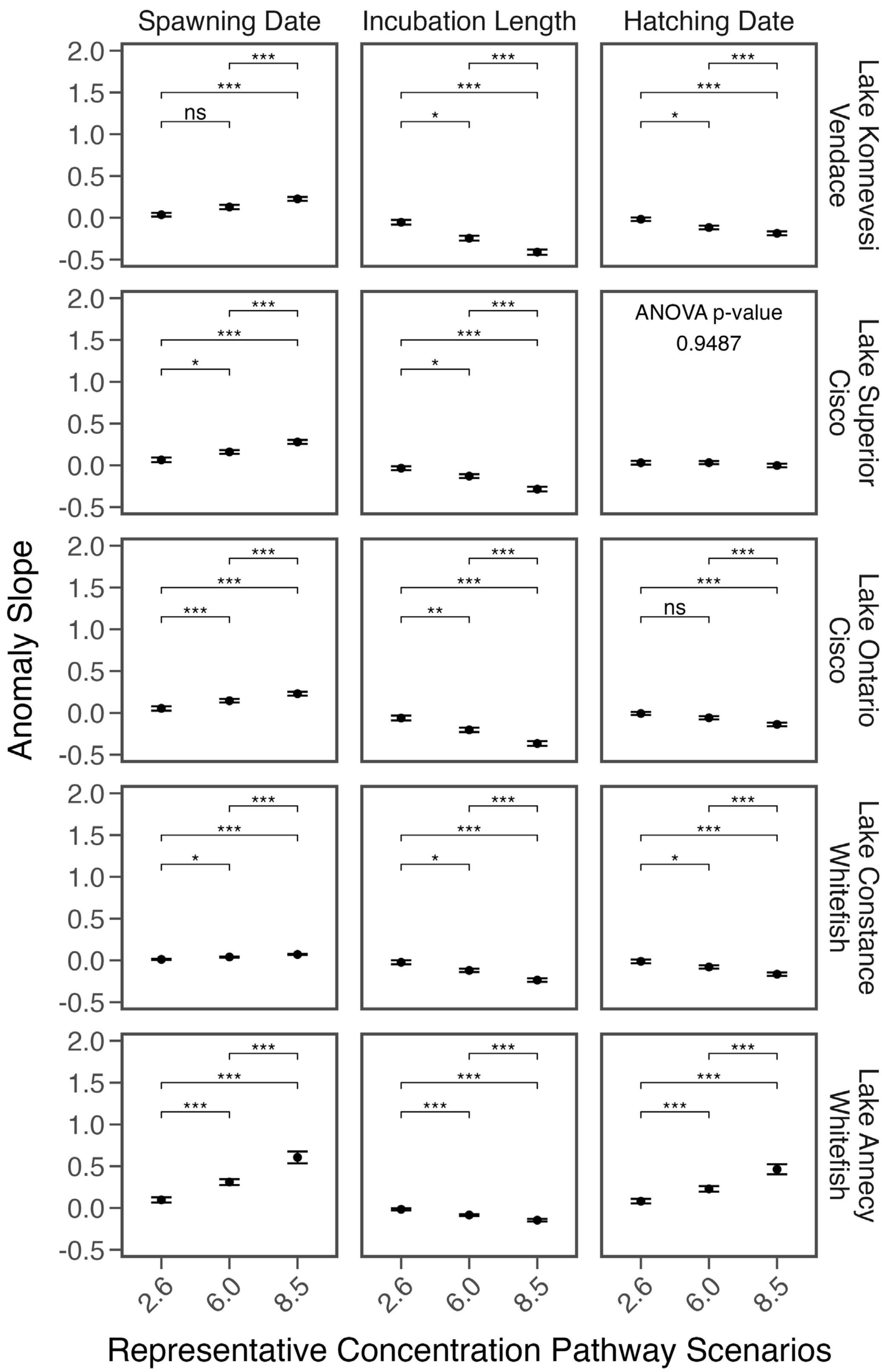

Fig. 6. Anomaly slopes for spawning date, incubation length, and hatching date among representative concentration pathway (RCP) scenarios. Study groups included vendace (*Coregonus albula*), cisco (*C. artedi)* from lakes Superior and Ontario, the littoral species of European whitefish (*C. lavaretus*) from Lake Annecy, and the pelagic species of European whitefish (*C. lavaretus*) from Lake Constance. The *p*-value from Tukey post-hoc pairwise comparisons within each study group is provided if the RCP p-value from the two-way ANOVA main effect was significant. Error bars indicate 95% confidence interval. *** <0.001; ** <0.01; * = <0.05; ns = Not Significant (>0.05).

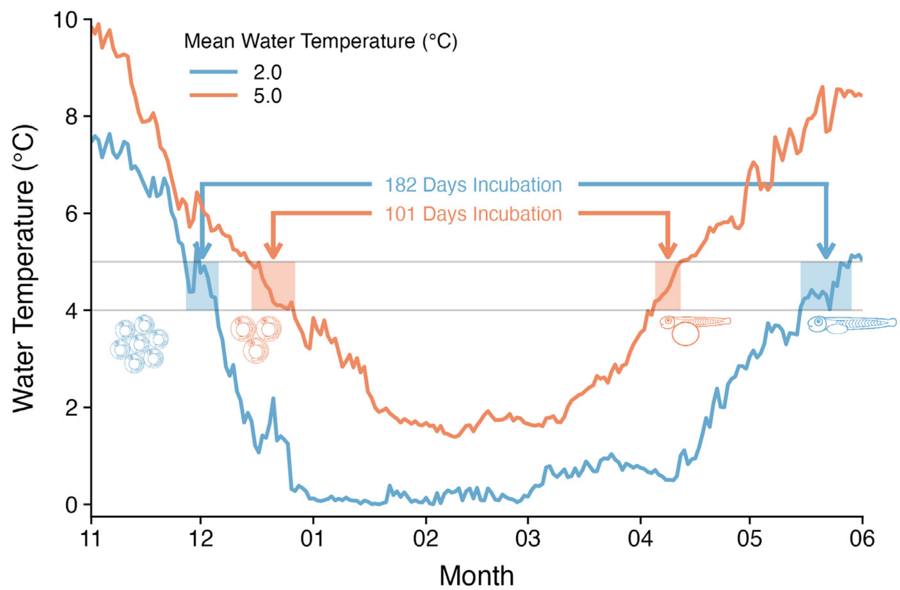

Fig. 7. Theoretical winter incubation periods and responses of embryo demographics under normal (2.0 °C; blue) and hypothetical warm (5.0 °C; orange) winter thermal regimes. The shaded regions indicate spawning periods (left) and hatching periods (right) that may occur between 4 and 5 °C. The 2.0 °C temperature regime is water temperature data collected from Lake Superior at 10-m depth in 2018.

8.5 scenario for all study groups (mean decrease = 0.29 days year^{-1}). Incubation length had similar responses within the RCP 8.5 scenario to increased temperatures among all study groups, with vendace from Lake Southern Konnevesi having the greatest response (–0.41 days year^{-1}) and the pelagic species of European whitefish from Lake Constance having the smallest response (-0.24 days year^{-1}; Figs. 4 and 5). Furthermore, all study groups responded similarly to increased temperatures within the RCP 6.0 and 2.6 scenarios (mean = -0.16 and -0.04 days, respectively). All RCP anomaly slope pairwise comparisons were significant for incubation length within each study group ($p < 0.05$; Fig. 6).

3.3 Hatching

Model simulation outputs for hatching date were variable among study groups (Figs. 4 and 5). Hatching dates of cisco from Lake Ontario, vendace from Lake Southern Konnevesi, and the pelagic species of European whitefish from Lake Constance were earlier in response to increased temperatures, while hatching dates of European whitefish from Lake Annecy were later and did not change for cisco from Lake Superior as water temperatures increased. The hatching date anomaly slopes among RCP scenarios were not significantly different for cisco from Lake Superior ($p = 0.949$). RCP anomaly slope pairwise comparisons between RCP 2.6 and 6.0 for Lake Ontario cisco ($p = 0.259$) were not significant. All other comparisons were significant ($p < 0.05$; Fig. 6).

4 Discussion

Our hypothesis that delays in coregonine spawning, as a consequence of changes in autumn and winter cooling, would result in altered embryo incubation durations (*i.e.*, number of days between spawning and hatching) and hatching times was supported for all study groups. Simulation models predicted that climate-induced increases in water temperatures will shift reproductive phenology of coregonines causing (1) delayed spawning, (2) shorter embryo incubation durations, and (3) varying changes to larval hatching dates (Fig. 7). Relative changes were higher with more severe climate change scenarios for littoral species where embryos have higher contemporary incubation water temperatures (*e.g.*, European whitefish from Lake Annecy).

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

Shifting reproductive timing is a plausible response to warming temperatures. Contemporary coregonine populations exhibit multiple spawning strategies ranging from autumn to spring-spawning stocks (Eronen and Lahti, 1988; Hénault and Fortin, 1991; Schulz *et al.*, 2006; Ohlberger *et al.*, 2008). Thermal habitat used by high-latitude or deep-spawning populations could be less affected by climate change and may still provide adequate spawning and incubation conditions if water temperatures continue to rise, but this may not be the case for low-latitude or littoral-spawning populations. For example, Lake Annecy is near the southern native extent for European whitefish and had the largest shift in spawning time among our study groups, but adequate thermal spawning temperatures were absent by the middle of the 21st century under the worst-case climate scenario. This projection is likely to be applicable for populations within the same geographic region that inhabit lakes with similar morphology and thermal conditions where population-specific DR_{50} models were not able to be validated, and even more dire projections could be expected for non-native populations south of Lake Annecy (*e.g.*, Lake Garda [Italy]; Volta *et al.*, 2018). However, these southern European lakes are deep (>80 m) with stable thermal refugia outside of the littoral zone (Kelly *et al.*, 2020). Shifting spawning strategies to use deeper habitats could provide adequate thermal conditions for ovulation to initiate, but whether suitable coregonine spawning habitat is available in these deeper waters, including sufficient oxygen levels, is unknown (Jane *et al.*, 2020; Kelly *et al.*, 2020; Desgué-Itier *et al.*, 2023).

Spawning scenarios determined many of the changes in reproduction phenology but embryos are static and unable to evade changes in winter water temperatures post-spawning (Stockwell *et al.*, 2014). Elevated incubation water temperatures accelerated embryo rates of development and hatching time and were not negated by delayed spawning. The frequency of shorter, warmer winters is projected to increase (Sharma *et al.*, 2019), which corresponds with our simulation results suggesting future incubation durations will decrease across all study groups. In the absence of changes to spawning behavior or habitat, warmer and shorter incubations could cause higher coregonine embryo and larvae mortality, increased occurrence of embryo deformities, and smaller and less robust larvae at hatching compared to colder, longer incubations (Stewart *et al.*, 2021a,b). Additionally, reduced ice formation caused by warmer air and water temperatures could decrease embryo survival from increased storm displacement and sediment deposition while decreasing lengths-at-hatching (Kangur *et al.*, 2020; Stewart *et al.*, 2021b). A complex mix of environmental factors during embryogenesis could generate high variability in hatching success and larval fitness - this was not considered in our modeling efforts (Hjort, 1914; Houde, 1989; Marjomäki *et al.*, 2004; Fig. 7).

Coregonine populations where embryos incubate in cold littoral waters (<4 °C) are hypothesized to rely on ice-break up and spring warming to trigger final embryo development stages and hatching (Karjalainen *et al.*, 2015). The rapid increase in spring water temperatures also synchronizes other phenological processes such as the onset of spring plankton blooms (Sommer *et al.*, 2012). Our simulations suggest significant changes in length of incubation and subsequent hatching times, and changes in thermal regimes and time of hatching may result in temporal separation between coregonine larvae and their zooplanktonic prey. Increases in seasonal temperature variability could also cause mismatches with larval zooplankton prey if temperature changes are not heterogeneous across seasons *(e.g.*, a cold winter followed by a warm spring; Straile *et al.*, 2015).

Fish year-class strength is often dependent on larvae surviving from hatch through the first three to six months of life and successfully transitioning from endogenous to exogenous feeding (Hjort, 1914; Houde and Hoyt, 1987; Cushing, 1990). Numerous size-dependent processes strongly influence when larvae need to first feed and their ability to successfully forage (Miller *et* al., 1988). Coregonine larval body size at hatching is inversely related to incubation water temperature, and length-at-hatch and yolk-sac volume have a negative relationship (Karjalainen *et al.*, 2015; Stewart *et al.*, 2021a). Warmer incubations result in coregonine larvae hatching earlier with smaller lengths and larger yolk-sacs (Stewart *et al.*, 2021a). Increased yolk-sac energy reserves at hatching may help larvae reduce starvation risk but the rate of endogenous feeding (*i.e.*, yolk consumption) is regulated by metabolic demand (Kamler, 2008). Earlier and warmer spring water temperatures in nursery zones, which induce earlier hatching, could accelerate yolk consumption in newly hatched larvae and counteract the physiological trade-off between length-at-hatching and yolk-sac volume. Larvae hatching earlier in the spring may also have reduced swimming abilities, reduced visual acuity, and more gape limitations, which can impact their ability to evade predators and forage efficiently (Miller *et al.*, 1988; Myers *et al.*, 2014). Determining the physiological stress response of hatching earlier and the impact warming nursery water temperatures may have on yolk conversion efficiency is a logical and necessary next step to build on our simulation results.

Our models extend earlier approaches (Colby and Brooke, 1973; Luczyński and Kirklewska, 1984; Eckmann, 1987) by incorporating mechanistic relationships to future climate-change scenarios from a wider range of populations. Because coregonines are highly developmentally plastic and exhibit diverse spawning behaviors (Muir *et al.*, 2013), the transferability of published models to other populations appears limited. High-quality *in situ* reproductive and embryo development data are critical to fitting and validating new population-specific development models. For example, hatching data for European whitefish in Lake Geneva were only available for a single year with a limited sampling period and likely did not capture the start of hatching. This led to development models underestimating hatching when, in reality, the *in situ* data likely did not represent the true hatching period and created a limitation in our modeling efforts. Increasing field sampling efforts around these critical life stages will benefit future research and climate-change predictability for both applied and modeling-based methods. Our simulations demonstrated that subtle changes in water temperature could translate into substantial changes in the reproductive phenology of coregonines among our study groups. Long-term changes in environmental conditions during reproductive and development periods could play a large role in generating variability in offspring success (Houde and Hoyt, 1987; Little *et al.*, 2020). The results of our modeling efforts highlight how water temperature is fundamental in regulating biological and physiological processes, but the impact of these changes is difficult to decipher as coregonines are behaviorally and developmentally plastic (Muir *et al.*, 2013; Karjalainen *et al.*, 2015). Quantifying the relationships between water temperature and coregonine reproductive phenology across a wide range of populations will be useful for managers to determine which populations may be more susceptible to the consequences of climate change and help prioritize conservation and restoration efforts. Unless coregonines exhibit behavioral or thermal adaptations to changing environmental conditions (*e.g.*, McQuinn, 1997; Jørgensen *et al.*, 2006), we expect that the changes in coregonine reproductive phenology predicted by our models will have negative implications for population sustainability throughout the 21st century, even under the lowest climate-emission scenario.

APPENDIX A

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

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

Table A.2. Study group and modeled case-study lakes from inter-sectoral impact model intercomparison project that match study group parameters (the lakes that were averaged together by category).

Lake type	Lake name	Latitude	Longitude	Climate zone	Depth bin (m)
Group Study	Geneva	46.37	6.45	Northern Temperate	0–10
	Annecy	45.86	6.17	Northern Temperate	0–10
	Ontario	44.05	−76.20	Northern Temperate	0–10
	Superior (Thunder Bay)	48.41	−89.02	Northern Temperate	10–25
	Superior (Apostle Islands)	46.85	−90.55	Northern Temperate	10–25
	Constance	47.64	9.38	Northern Temperate	50+
	Southern Konnevesi	62.58	26.58	Northern Cool	0–10
Modeled Case Study	Mueggelsee	52.43	13.65	Northern Temperate	0–10
	Allequash	46.04	−89.62	Northern Temperate	0–10
	Trout Bog	46.04	−89.69	Northern Temperate	0–10
	Crystal Bog	46.01	−89.61	Northern Temperate	0–10
	Wingra	43.05	−89.43	Northern Temperate	0–10
	Esthwaite-Water	54.37	−2.99	Northern Temperate	10–25
	Big Muskellunge	46.02	−89.61	Northern Temperate	10–25
	Sparkling	46.01	−89.70	Northern Temperate	10–25
	Crystal Lake	46.00	−89.61	Northern Temperate	10–25
	Two-Sisters	45.77	−89.53	Northern Temperate	10–25
	Dickie	45.15	−79.09	Northern Temperate	10–25
	Great	44.53	−69.89	Northern Temperate	10–25
	Fish	43.29	−89.65	Northern Temperate	10–25
	Mendota	43.10	−89.41	Northern Temperate	10–25
	Delavan	42.61	−88.60	Northern Temperate	10–25
	Stechlin	53.17	13.03	Northern Temperate	50+
	Rappbode	51.74	10.89	Northern Temperate	50+
	Kuivajarvi	60.47	23.51	Northern Cool	0–10
	Vortsjaerv	58.31	26.01	Northern Cool	0–10
	Nohipalo–Mustjaerv	57.93	27.34	Northern Cool	0–10
	Laramie	40.62	−105.84	Northern Cool	0–10

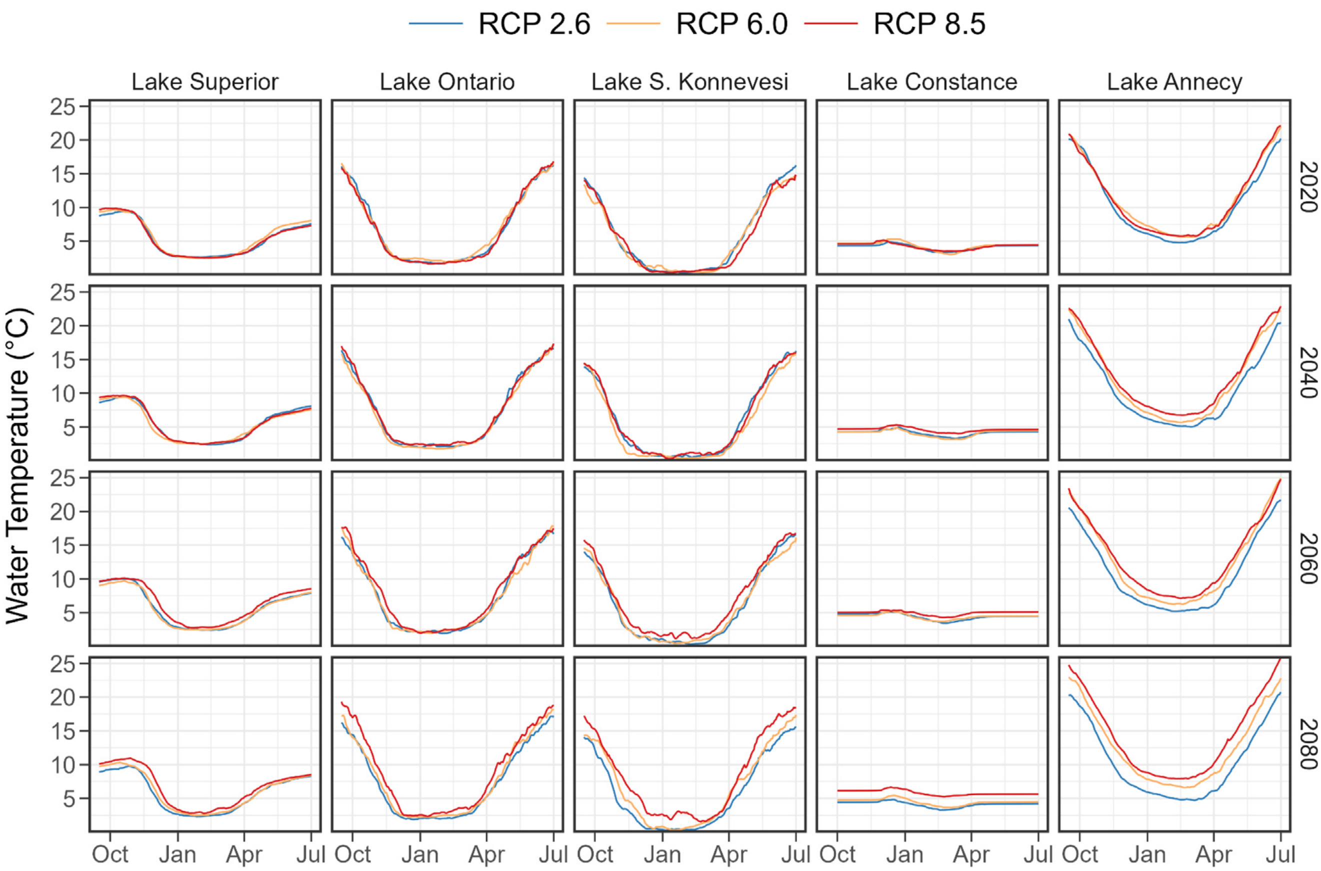

Fig. A.1. Simulated daily lake bottom water temperatures for three representative concentration pathways (RCP) in 2020, 2040, 2060, and 2080 for Lake Superior, Lake Ontario, Lake Southern Konnevesi, Lake Constance, and Lake Annecy.

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