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Coldwater, stenothermic fish seem bound to suffer under the spectre of future warming

Barnaby John Roberts [a,b,*], Christoph Chucholl [b], Alexander Brinker [a,b]

[a] University of Konstanz, Institute for Limnology, Mainaustraße 252, 78464 Konstanz, Germany
[b] Fisheries Research Station Baden-Württemberg, Argenweg 50/1, 88085 Langenargen, Germany

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ABSTRACT

Climate change has the potential to impact lacustrine fish populations by affecting both their physiologies and phenologies. Coldwater, stenothermic fishes that spawn in winter may be at the highest risk of being negatively impacted by predicted future climate warming. To investigate this subject, we tested the impact of temperature on the embryonic and larval stages of coldwater, stenothermic salmonid whitefishes (coregonines). Embryos of two coregonine species from Upper Lake Constance (a large, deep perialpine lake bordering Austria, Germany and Switzerland) were incubated at three temperatures approximating historic and potential future water temperatures. After hatching, larvae from all incubation treatments were transferred to two rearing temperature treatments. Hatching times were advanced by higher temperatures, whilst mortality and larval performance responses to higher temperatures were generally negative, suggesting that future climate warming will reduce coregonine recruitment in Upper Lake Constance. The two species tested varied in their specific responses to temperature and in the sensitivity of their responses to temperature. Additionally, we found that incubation temperature affected the performance of coregonine larvae up to two and a half months after hatching. Using our data on hatching times, we infer that future climate change could advance coregonine phenologies in Upper Lake Constance by up to two weeks by the end of the 21st century.

1. Introduction

Ongoing climate change may profoundly impact the survival and fitness of individuals in a population through various mechanisms, potentially driving species into local extinction (Román-Palacios and Wiens, 2020). Being ectothermic organisms with life cycles closely linked to local climatic conditions, freshwater fishes are particularly vulnerable to changing temperature regimes (Comte and Olden, 2017; Basen et al., 2020). For instance, rising ambient temperatures may directly affect fish survival, especially during early life stages that are adapted to a narrow range of temperatures (Heino et al., 2015), or desynchronise interspecific phenological relationships (Visser and Gienapp, 2019).

Higher water temperatures can reduce fish recruitment by increasing embryonic mortality (Ojanguren and Braña, 2003; Lahnsteiner et al., 2012; Martin et al., 2020). They can also shorten the period larvae feed endogenously and alter larval migration patterns (Raventos et al., 2021; Russel et al., 2022). Incubation temperature can influence an individual's characteristics, including growth rates (Burgerhout et al., 2017), physiological processes (Perrichon et al., 2018), body composition and gene expression (Scott and Johnston, 2012; Burgerhout et al., 2017), throughout larval and later life stages. Overall, the suite of fitness-related traits influenced by temperature experienced during embryogenesis and early life (Jonsson and Jonsson, 2014; Jonsson and Jonsson, 2019) indicates that although some species might adapt to future climate warming, many species may be negatively affected (Alix et al., 2020; Dahlke et al., 2020; Basen et al., 2022).

In addition to direct effects on individual fitness and survival, climate change may decouple phenological events. The match/mismatch hypothesis states that a good phenological match between consumers, such as fish larvae, and resources that they consume, such as zooplankton, is vital for effective consumer recruitment (Ferreira et al., 2020; Trochta et al., 2020). In contrast, a mismatch between consumers and resources can result in poor consumer recruitment (Cushing, 1990). Generally, during a mismatch, ambient water temperatures cause fish larvae to hatch too early or late to access suitable zooplankton densities, resulting in decreased larval survival. Studies focusing on single (Régnier et al., 2019; Brossett et al., 2020; Ferreria et al., 2023; Moyano

* Corresponding author at: Fisheries Research Station Baden-Württemberg. Argenweg 50/1, 88085 Langenargen, Germany.
E-mail addresses: barnaby.roberts@lazbw.bwl.de (B.J. Roberts), christoph.chucholl@lazbw.bwl.de (C. Chucholl), alexander.brinker@lazbw.bwl.de (A. Brinker).

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et al., 2023) and multiple fish species (Durant et al., 2019) support the validity of the match-mismatch hypothesis. Predicted future warming increases the probability of mismatches between fish larvae and zooplankton occurring (Asch et al., 2019; Durant et al., 2019).

The endemic coldwater, stenothermic whitefish (*Coregonus* spp., Coregonineae Salmoniformes; also coregonines) of Lake Constance are flagship species of high ecological and socio-economic importance (Baer et al., 2017). Lake Constance is a 536 km^2 perialpine lake with a maximum depth of 252 m that borders Austria, Germany and Switzerland. The lake is divided into an oligotrophic 473 km^2 upper lake (Upper Lake Constance) and a 61 km^2 mesotrophic lower lake (Lower Lake Constance), which are connected by a river-like body of water known as the Seerhein ('Lake Rhine' in English). The immediate Lake Constance region has a current human population of over 4 million, and the lake experienced strong eutrophication and reoligotrophication throughout the 20th century (Baer et al., 2017). Indeed, eutrophication-induced hypoxia may have been the main driver for the extinction of an endemic deep-water 'dwarf' coregonine, *Coregonus gutturosus* (Gmelin, 1818), known locally as Kilch (Frei et al., 2023). The mixing regime of the lake is monomictic, with mixing normally occurring during February and March. Extensive ice cover is extremely rare, with the last full freezing of Upper Lake Constance's surface occurring in 1963 (Sommer, 1985; Peeters et al., 2007).

Coregonines are naturally dominant species within Lake Constance's pelagic food web and support one of the most important European inland fisheries, which is characterised by a high demand for endemic *Coregonus* spp., known locally as Felchen. The two coregonine species most important to the Upper Lake Constance fishery, and historically dominant in terms of number and biomass, are the pelagic feeding, pelagic spawning *C. wartmanni* (Bloch, 1784) and the benthic feeding, littoral spawning *C. macrophthalmus* (Nüsslin, 1882). Both species are medium-sized coregonines that spawn during winter and exhibit lek-spawning behaviour. The pelagic *C. wartmanni* spawns over the deepest parts of the lake. Courtship and spawning occur when large swarms of *C. wartmanni* gather in open surface waters. Spawning usually occurs within one to two weeks, with peak spawning most often occurring at the beginning of December. Peak spawning of *C. macrophthalmus* generally occurs in early December, but spawning can occur from as early as mid-November until January. Spawning occurs near the sediment, in depths ranging from 5 m to around 100 m (Frei et al., 2023). Both species spawn over fine sediment, which ranges from sandy loam in shallower areas to silty clay in the deepest parts of the lake (Schmitz, 1971). Another extant, endemic (described) coregonine, *C. arenicolus* (Kottelat, 1997), as well as an undescribed, potamodromous coregonine species (or potential ecotype), *Coregonus* sp. 'Alpenrhein', are found in Upper Lake Constance.

Due to their physiology and evolutionary history, Lake Constance coregonines are among the species that might be negatively affected by warming (Trippel et al., 1991). An embryogenesis study of Lake Constance coregonines showed that a 3 °C temperature increase accelerated hatching times by 30–42 % (Eckmann, 1987). Studies of other coregonines show that temperature increases of ~4 °C can reduce embryo survival by more than 25 % (Cigni et al., 2010; Mueller et al., 2015; Stewart et al., 2021). Incubation temperature's effects extend beyond embryogenesis, affecting the mortality and growth of coregonine larvae (Steinbacher et al., 2017; Stewart et al., 2022). Furthermore, sympatric coregonines' responses to temperature during embryonic, larval and later life stages vary (Eckmann and Pusch, 1989; Ohlberger et al., 2008; Steinbacher et al., 2017; Stewart et al., 2021). Thus, evidence suggests climate warming could reduce coregonine recruitment and modulate early life history via both phenological and physiological mechanisms.

If the phenologies of different trophic levels in Lake Constance advance simultaneously, trophic mismatches may not occur (Straile et al., 2015). However, synchronisation between different food web members cannot be guaranteed (Vadidi–Fülöp and Hufnagel, 2014), and the influence of lower trophic level biomass on fish populations varies (Nõges et al., 2018). Due to warming in Lake Constance, the timing of spring phytoplankton blooms and the onset of the clear–water phase (late spring/early summer chlorophyll minima) has already advanced (Straile, 2002; Shimoda et al., 2011). Continued warming is predicted to advance spring plankton blooms in the future (Gronchi et al., 2021); this might reduce the time window when copepod nauplii, which might be important for coregonine larval survival (Santer and Lambert, 1995; Myers et al., 2014), are available. Therefore, despite some uncertainties, research indicates that warming could reduce the chance that coregonine larvae find sufficient, suitable food.

Understanding how temperature affects the early life stages of Lake Constance coregonines is of major value because the lake's coregonine stocks have already undergone substantial contraction in recent years (Baer et al., 2017; Baer and Brinker, 2021). Factors which have likely contributed to this decline include a reduction in primary production (Baer et al., 2017) and the impacts of invasive species, particularly three–spined stickleback (*Gasterosteus aculeatus*) (Roch et al., 2018; Rösch et al., 2018; Gugele et al., 2020; Ogorelec et al., 2022) and quagga mussel (*Dreissena rostriformis bugensis*) (Baer et al., 2022a). Climate change might further worsen the situation and warrants investigating how temperatures impact the early life stages of Lake Constance coregonines.

Here, we present a study on temperature's impacts on the embryonic and larval life stages of the two dominant coregonine species (*C. wartmanni* and *C. macrophthalmus*) in Upper Lake Constance (ULC). We incubated embryos (wild offspring) under three temperatures (ranging from historical to potential future winter water temperatures). After they hatched, we reared offspring from all incubation treatments in unheated and heated water. Based on our literature research, we assumed that higher temperatures would reduce the time before Lake Constance coregonines hatch and would increase embryo mortality. Both incubation temperature and the temperature larvae are reared in should also impact larval mortality and growth. Lastly, we expect sympatric coregonine species to react to temperature differently. More specifically, we expect *C. wartmanni*, a species in which embryos develop in deeper, and hence generally cooler, less thermally variable water, will be more sensitive in its responses to higher temperatures. But *C. macrophthalmus*, which spawns in shallower, and hence generally warmer, more thermally variable water, should be better adapted and more resilient to higher temperatures.

2. Methods

2.1. Embryo collection and fertilisation

On 28.11.2021, gill nets (38–44 mm mesh width) were set to capture wild *C. wartmanni* and *C. macropthalmus*: referred to in this article, respectively, by their local names, Blaufelchen and Gangfisch. More than a century of regular sampling during the spawning season means that employees working at the Fisheries Research Station Baden–Württemberg have acquired significant local knowledge on the best locations to successfully catch spawning individuals. Baufelchen are caught in a large pelagic area, with nets generally being set in water over 100 m deep. Known Gangfisch spawning sites, in the vicinity of a river mouth and on the edge of the lake shelf, were selected as locations to capture Gangfisch. Blaufelchen were caught in water around 130 m deep (DD coordinates: 47.574441, 9.409103), using nets that were suspended between 6–12 m depth. Gangfisch were caught in water 20 m deep (47.610445, 9.513559) using nets set on the lake sediment. More female fish (Blaufelchen $n = 25$; Gangfisch $n = 30$) were caught than male fish (Blaufelchen $n = 8$; Gangfisch $n = 10$), perhaps because female fish are more rotund during the spawning season. Mean length of the two species did vary (Chi square = 9.69, $p = .0019$, $df = 1$) by 2 cm (Blaufelchen = 34.8 cm; Gangfisch = 32.8). The generally smaller Gangfisch males (Chi square = 12.38, $p = <.0001$, $df = 1$) caused this difference (Blaufelchen = 34.5 cm; Gangfisch = 30.5): females showed no statistically

significant interspecific variation in size (Blaufelchen = 34.9 cm; Gangfisch = 33.6). Age did not vary (statistically) between Blaufelchen (mean = 3.9) and Gangfisch (mean = 3.7). Mean egg size (diameter) did differ between the two species ($t(94.8) = -2.30$, $p = 0.0237$), but only by around 0.1 mm (Blaufelchen = 2.74 mm; Gangfisch = 2.82 mm). Nets were collected from the lake between 8 and 10 am on 29.11.2022. Immediately after capture, gametes were stripped from sires and dams. Next, these stripped gametes were mixed in plastic buckets using the 'dry' method (developed by Vrasski: Slack, 1872; Capel, 1885). The fertilised embryos were not disinfected, so that the embryos' natural microbiome was not artificially altered.

The embryos were brought to a professional hatchery in Langenargen, Germany. Embryos were kept in the buckets they were fertilised in, which were filled with lake water to allow the eggs to harden. At around 4 pm, the fertilised embryos were transferred into glass incubation jars. Incubation jars received a constant flow of sand–filtered water directly from ULC, which rolled the embryos continuously. Hatch dates of embryos kept in incubation jars were recorded. We recorded incubation times in the hatchery for two reasons: 1) to provide a 'back-up' experiment if our main experiment somehow failed and 2) to compare the different incubation methods. Dead embryos were removed with a feather, but mortality was not systematically recorded. Incubation jars were kept in the main room of the hatchery building which was illuminated by artificial (during working hours) and natural light. Further details of how hatch dates in the incubation jars were recorded are given in the Appendix (Electronic Supplementary Material (ESM) Appendix S1).

2.2. Transfer of embryos to the main experimental set-up & embryo care

Three days after fertilisation, a portion of the embryos (of both species) were removed from the incubation jars and brought into three climate-controlled chambers in the Fisheries Research Station, Langenargen, Germany. Chambers were maintained at temperatures that approximated realistic past, current and potential future winter water temperatures in ULC: 4.3–4.4 °C ($SD = 0.7$ °C), 6.6 °C ($SD = 0.4$ °C) and 8.3 °C ($SD = 0.1$ °C), respectively. In the period from 1981 to 2010, winter water temperatures in ULC were, on average, 5.7 °C at 20 m depth (typical Gangfisch spawning depth), 4.8 °C at 100 m (spawning depth of Blaufelchen and Gangfisch) and 4.5 °C at 250 m (spawning depth of many Blaufelchen). In the data period prior to 1980, deeper-water (100 and 250 m) temperatures were regularly below 4.5 °C. Whereas in the last several years, deeper-water temperatures have regularly exceeded 5 °C and water temperatures at 20 m depth often exceed 6.5 °C. Furthermore, our predictions of future winter water temperatures (explained later in this article) indicate that temperatures at 20 m depth could surpass 8.3 °C at the end of the 21st century when following more carbon–intensive scenarios. Thus, the incubation temperatures we tested are biologically relevant. In this article, the tested incubation temperatures are also referred to as far–future (~8.3 °C), near–future (~6.6 °C) and historic (~4.3–4.4 °C).

Individual embryos were then transferred into 18 (per species) sterile Corning™ 24–well microplates; microplate wells each contained one embryo and were filled with 2.5–3 mL of lake water. Water in the microplate wells was not exchanged throughout the experiment. Every other day, microplates were checked for embryo mortalities, which were recorded and removed from the microplates. Four types of mortality were observed: bacterial infections, developmental abnormalities, 'fungal' infections (cf. *Sporaginella* sp.) and algal overgrowths. Mortality type was determined visually. Although the root cause of mortality could not be determined with certainty, regular checks and previous experience meant that specific mortality types were reliably determined. Apart from during mortality and hatching checks, when the chambers were illuminated with artificial light, the chambers were kept in total darkness. Further information on the main embryogenesis experiment set-up is in the Appendix (ESM Appendix S1.

2.3. Larval hatching and at-hatch larval measurements

Once larvae began to hatch, hatching and mortality were checked twice daily. Obvious deformations were recorded as hatch deformities. Hatch deformities were not measured or included in the larval growth set-up.

Hatched larvae were photographed using a microscope-camera system (VHX-700F, Keyence). Microscope photography allowed non-obvious deformations to be recorded, which were categorised as spinal or 'other'. Proprietary Keyence software was used to record length–at–hatch (total length) and the height and length of the larvae's yolk sacs. Software recorded measurements in μm, which were converted to the nearest .01 mm. Yolk-sac length and height were used to calculate larvae yolk-sac volume (mm^3), assuming that yolk sacs were ellipsoid.

$$YSV = \frac{\pi}{6} ab^2$$

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

2.4. Larval growth experimental set-up

After larvae began hatching in significant numbers, they were transferred to 65 L tanks in the professional hatchery. There were twelve aquaria in total; equal numbers of each species (from each incubation treatment) were transferred into two temperature treatments. Larvae (95 or 100) were transferred over a number of days (5–14) during the period of peak hatching. Tanks had a constant flow of lake water, either unheated ($M = 6.9$ °C, $SD = 0.6$ °C) or heated ($M = 8.9$ °C, $SD = 0.2$ °C): referred to in this article as lake (6.9 °C) and warmed (8.9 °C). Further details on transfer into the larval growth experiment set-up are given in ESM Appendix S1.

After some larvae had almost used up their yolk sac reserves, they were fed unenriched *Artemia franciscana* 2–3 times daily (Artemia Eier A+, Algova). Each day, uneaten *Artemia* nauplii and dead larvae were removed with a siphon, and mortality was recorded. Final larval mortality is expressed as a percentage.

Yolk-sac absorption time was estimated visually from the day after larvae were first fed by catching 10 larvae in a glass beaker and inspecting them visually. Daily, yolk–sac presence or absence was noted until no larvae inspected had yolk sacs. Values of yolk-sac absorption time used are the number of days from when the last larvae were transferred into the tank until all 10 larvae inspected were observed to have no yolk sac remaining. Further information on how yolk sac absorption was recorded is in ESM Appendix S1.

The experiment ran 81 days after the date that 50 % of the larvae had been transferred into that tank. Therefore, larvae were 'on average' 81 days old, with a roughly equal number of younger and older larvae also being present. Larvae were euthanised using and overdose of clove oil and fixed in 99 %+ ethanol (Absolute, Extra Pure, SLR, Fisher Chemical™). Later, 30 larvae from each aquarium were measured to the nearest 0.1 mm (total length) and weighed to the nearest 0.0001 g (wet weight).

Several larval growth and performance measures were calculated to provide information on larval growth. The Specific Growth Rate (SGR) of length and weight was calculated as follows:

$$SGR^L\ (\%) = 100 \times [(lnL_t - lnL_0)/d]$$

$$SGR^W(\%) = 100 \times [(\ln W_t - \ln W_0)/d]$$

Where L_t and L_0 are, respectively, the final length and length-at-hatch of larvae. W_t and W_0 are the final weight and weight-at-hatch of larvae, respectively. The larvae's average age, in days-post-hatch, is given by d and ln is the natural logarithm. Average length–at–hatch (mm) values, during the window of transfer into an aquarium, were calculated. Then, by using unpublished length-weight data from wild ULC coregonine

yolk–sac larvae (to produce a length-weight relationship regression), these length–at–hatch values were converted to weight-at-hatch (g) values using the following formula

$$W_0 = \exp(-10.478 + 2.081 \times \log L_0)$$

where W_0 equals weight-at-hatch, L_0 equals length-at-hatch and log is the decadic logarithm.

The Thermal Growth Coefficient (TGC) of larvae was calculated as follows:

$$TGC = \sqrt[3]{W_t} - \sqrt[3]{W_0} \times \left(\sum T\right) \times 1000$$

where W_t and W_0 are the final weight and weight-at-hatch of larvae, respectively, and Σ^T is the total accumulated-degree-days, i.e. the total number of degree days larvae experienced from the date of average hatch (the date when 50 % of larvae were transferred into that aquarium) in that aquarium until 81 days post-average-hatch. Degree days were always calculated using a base temperature of 0 °C.

The Feed Conversion Efficiency (FCE) of each tank was calculated as follows:

$$FCE = \frac{Total\ biomass\ produced\ (g)}{Total\ feed\ given\ (g)}$$

Total feed given was the daily weight of *Artemia* nauplii fed to each tank multiplied by the number of days larvae were fed. 'Total biomass produced' took mortality into account. The growth rate (mm) per day was calculated for each tank: length-per-day growth rates of ULC coregonines are linear (Thomas and Eckmann, 2012). Length–per–day growth rates were used to calculate larvae's length-at-death. Then a length–weight relationship regression formula, produced using wild ULC coregonine larvae length-weight data, was used to calculate weight-at-death as follows:

$$W_t = \exp(-13.417 + 3.314 \times \log L_t)$$

where W_t equals weight-at-death, L_t equals length-at-death and log is the decadic logarithm.

Mean values of larval weight per aquarium were calculated and then multiplied by the number of surviving larvae in that aquarium. The total calculated weight of dead larvae was added to this value, and the initial weight of larvae was subtracted, giving a value of total biomass produced.

2.5. Statistical analysis of study data

Most data were analysed with suitable linear models, following a model selection process. In each case, residuals of final models were inspected for constant variance, independence and normality. Hatching dates were analysed using linear mixed models, and nearly all other response variables were analysed using least-squares regressions (Sokal and Rohlf, 1981). Hatching date models used the date (days-post-fertilisation) or sum of degree-days (post-fertilisation) when an individual larva hatched within a microplate well as the response variable value. Hatching date (days-post-fertilisation and accumulated–degree–days. i.e.. the sum of degree-days) mixed models included incubation microplates (nested within incubation chamber) as a random factor.

Models that dealt with embryogenesis (hatching dates) and at-hatch larval morphometrics (length–at–hatch and yolk–sac volume) used species, incubation temperature and their interaction as explanatory variables. A residual pseudo–likelihood method of parameter optimisation was used for the hatching date mixed models (Wolfinger and O'Connell, 1993). The coefficient of variance was used to compare hatch date distributions. To compare our findings with a past study of ULC coregonine embryogenesis, we utilised a model from Eckmann (1987), and used the temperatures from our embryogenesis experiment to calculate the predicted time (days-post-fertilisation) to median hatch. Student's *t*–tests were used to test for significant differences between our study and Eckmann's hatch dates. We tested hypothetical median hatch dates calculated using the model from Eckmann (1987) against the mean hatch dates from our raw data. These tests can be considered valid as mean and median hatching dates in our data never differed by more than one day. The model from Eckmann (1987) used to predict median hatching dates of Lake Constance coregonine species is as follows:

$$D = a - b \bullet \ln T$$

where D equals median hatching date, T equals average incubation temperature and ln represents the natural logarithm. Values of a and b, given in Eckmann (1987), for Blaufelchen and Gangfisch are given in the ESM S1. In addition, values using of a and b, using median hatch dates (per microplate) from this study, are also given in the supplementary materials. Median hatch date results using our data and that of Eckmann (1987) are summarised and compared in the ESM S1.

Embryonic mortality percentages were calculated for each microplate separately. These mortality percentages were the response variable used in the models that analyse temperature and species' effects on mortality. Hatch deformities were calculated as the proportion of hatched larvae and the proportion of the initial number of embryos. Collated values of all types of embryonic mortality (including hatch deformities), and all mortality types (excluding developmental abnormalities), were also calculated. Deformations observed using microscope photography were analysed using binary logistical models. The nominal level targeted in these models was 'yes' (i.e., the occurrence of a larva having a deformity). Least-squares regression models of at–hatch measurements and logistic regression models of at-hatch deformities (observed using the microscope) considered an individual larva as a replicate.

Yolk-sac absorption time explanatory variables included species, incubation temperature, aquarium temperature and the interaction between species and incubation temperature. This model used the yolk-sac absorption time in each aquarium as the response variable value. Larval mortality, growth and performance measure models included species, incubation temperature, aquarium temperature and all possible interaction effects between these explanatory variables as model effects. Larval mortality and Feed Conversion Efficiency Ratio values were calculated for each aquarium and used as the response variable values. Other growth and performance measures were calculated from the sample of 30 individuals taken from each aquarium, and individual larvae were considered replicates. All statistical analysis was performed in JMP Pro (SAS Institute, Version 17.1.0). Student's *t*-tests were used to test for differences between species. Independent resampled units were used to assess the importance of explanatory variables used in linear mixed models, with total effect values being reported. For least-squares regressions, eta-squared (η^2) is used to assess effect size.

2.6. Estimations of future water temperature and hatching dates of coregonines in Upper Lake Constance

The hatching dates and yolk sac absorption models were used to evaluate the possible impacts of future climate warming on ULC coregonine's early-life phenologies, including the timing of when larvae absorb their yolk sacs and begin exogenous feeding. Mean hatch dates were added to mean yolk sac absorption times to produce a value of the average number of days post-fertilisation to full yolk-sac absorption.

We used generalized linear models, which used historical local air temperature (Konstanz, Germany) data as explanatory variables (annual average air temperature and coldest quarter air temperature) and ULC water temperature data (at four depths) as a response variable. The calibration dataset with observation values for both air and water temperature extended from 1973 to 2022.

The CHELSA climate database (https://www.chelsa-climate.org)

was used to extract historical climate information, spanning 1981–2010, and projected future air temperatures in the ULC area (Karger et al., 2017). Using five general circulation models, projections of annual average air temperature and coldest quarter air temperature were extracted for the future periods 2011–2040, 2041–2070 and 2071–2100 along three Shared Socioeconomic Pathways (ssp126, ssp370 and ssp585). We use the median value of general circulation model projections instead of the mean to avoid skew resulting from aberrant temperature predictions. The calibrated generalized linear models were then used to predict future water temperatures in ULC based on the projected future air temperatures. Water temperatures were predicted for the months relevant to the early–life stages of ULC coregonines (December-March).

We used ULC water temperature data at 20 m, 100 m and 250 m depths because of the ecological relevance of these depths to spawning coregonines. Most Blaufelchen spawn in the deepest part of the lake, meaning many Blaufelchen embryos develop at depths of around 250 m. The lake's average depth is 92 m, and the nearest depth available in the water temperature dataset was 100 m, which is relevant for shallower-spawning Blaufelchen. Gangfisch spawn near the lakebed in water 4 m to 90 m deep, with the highest spawner density at 20 m (Frei et al., 2023). Therefore, 20 m depth is relevant to most spawning Gangfisch, and 100 m depth relevant to deeper-spawning Gangfisch. Surface water (0 m depth) temperature is relevant to the yolk sac absorption stage because larvae approach and then stay near the surface until after they develop into juveniles (Braum, 1964; Eckmann and Putsch, 1989; Ventling–Schwank and Meng, 1995). Further details of the methods used to predict future temperatures are given in Appendix S1.

3. Results

3.1. Hatching dates

Higher incubation temperature significantly reduced the days-post-fertilisation (DPF) to hatch for both species. All explanatory variables proved to be statistically significant (Table 1). Incubation temperature had the largest effect on DPF hatching dates; species had a much smaller effect (Table 1). However, Blaufelchen and Gangfisch hatch dates did differ significantly; $t(107.1) = -26.23$, $p = <.0001$. Blaufelchen hatched 14 % (13 days) faster than Gangfisch at historic temperature. Blaufelchen also hatched 8 % (4 days) faster than Gangfisch at far-future temperature (Fig. 1).

The spread of DPF hatching dates was distinctly reduced at higher temperatures for both Blaufelchen and Gangfisch. Blaufelchen hatched over 39 days (69–108 DPF) at the historic incubation temperature and over 24 days (37–61 DPF) at far-future temperature. At historic incubation temperature, Gangfisch hatching occurred from 77 to 118 DPF (41 days), whilst at far-future temperature, hatching lasted from 45 to 60 DPF (15 days). Blaufelchen's coefficient of variation (CV) was 8.6 % at the coolest incubation temperature and 6.9 % at the highest ($p = 0.0262$). Gangfisch CV reduced from 7.2 % to 5.3 % between the coolest and warmest incubation temperatures ($p = 0.0238$).

The results of our study differed significantly from the results of a previous study of ULC coregonine embryogenesis performed by Eckmann (1987). In our study, hatching occurred consistently later (19–21 %) than predicted dates produced by the model presented in Eckmann's study (Table 2). At far-future temperature, both species hatched 10 days later than predicted hatching based on Eckmann's model. At the historic incubation temperature, Blaufelchen hatched 16 days later than Eckmann's prediction and Gangfisch 19 days later. These differences in hatch dates from our main embryogenesis experiment were significant (tested with *t*-tests) at every incubation temperature, for both species. In contrast, the hatch dates of embryos kept in incubation jars at the professional hatchery did not differ from predicted hatch dates produced using Eckmann's hatch model (Table 2).

3.2. Embryonic survival

Higher temperatures had an overall negative impact on embryonic survival, being a significant explanatory variable for all mortality types except developmental abnormalities (Table 3). 'Fungal' infections, algal overgrowths and hatch deformities were only affected by temperature, with higher temperature increasing the incidence of mortality (Table 3) although 'fungal' infections were uncommon and algal overgrowths rare. The temperature-dependent hatch deformity mortality was similar in both species (historic temperature = < .5%, far–future temperature = 2 %). Bacterial mortality responded positively to temperature, with all explanatory variables being significant (Table 3). Blaufelchen bacterial mortalities increased from an average of < .01 % at 4.3 °C to 2 % at 8.3 °C. Average Gangfisch bacterial mortality increased from near zero at the historic temperature to 12 % at the far-future temperature (Fig. 2). At far-future temperature, embryonic mortality followed an exponential trajectory characteristic of bacterial growth (Fig. 2; ESM Appendix S1, Fig. 5 (b)).

Developmental abnormality mortality varied between species (Table 3). Though, surprisingly, the relationship with temperature was positive. Blaufelchen mortality due to developmental abnormalities varied from 13 % at potential–future temperature to 18 % at historic temperature. Gangfisch developmental abnormality mortality varied only marginally between historic (19 %) and far–future temperature (18 %). All mortality types, excluding developmental abnormalities, collated provided the clearest picture of temperature's positive effect on mortality ($R^2 = .55$, $p = <.0001$). All independent variables significantly affected collated mortality (Table 3): both species increased from a low of < 1 % mortality at historic temperature to a high of 8 % for Blaufelchen and 18 % for Gangfisch at far-future temperature (Fig. 2).

Table 1
Results of linear mixed models examining the influence of temperature on hatching date measures for two species of Lake Constance coregonines (Blaufelchen and Gangfisch). Response variables are indicated in italics above the tested model effects. Temperature is a continuous variable. The date when an individual hatched (in a microplate well) was the response variable used in these models; the microplates in which individual embryos were incubated were considered as a random factor. Model effects which are statistically significant are highlighted in bold. Estimate = parameter estimate of model term coefficient; *SE* = standard error of parameter estimates; *t* = *t* ratio value (degrees of freedom, numerator degrees of freedom); *p* = *p*-value of *t*-test (alpha = <0.05); Importance = importance of non-interaction model effects assessed using independent resampled units.

Model and model effects	Estimate	*SE*	*t*	*p*	Importance
Days-post-fertilisation					
Intercept	**131.80**	**0.647**	**203.64 (1, 106)**	**<.0001**	–
Species	**−4.23**	**0.161**	**−26.23 (1, 107)**	**<.0001**	**0.07**
Temperature	**−10.06**	**0.099**	**−101.90 (1, 109)**	**<.0001**	**0.94**
Species*Temperature	**1.18**	**0.099**	**11.97 (1, 109)**	**<.0001**	–
Degree days					
Intercept	**390.82**	**4.91**	**79.49 (1, 103)**	**<.0001**	–
Species	**−24.00**	**1.22**	**−19.63 (1, 103)**	**<.0001**	**0.91**
Temperature	**4.08**	**0.75**	**5.45 (1, 105)**	**<.0001**	**0.10**
Species*Temperature	**3.01**	**0.75**	**4.03 (1, 105)**	**0.0001**	–

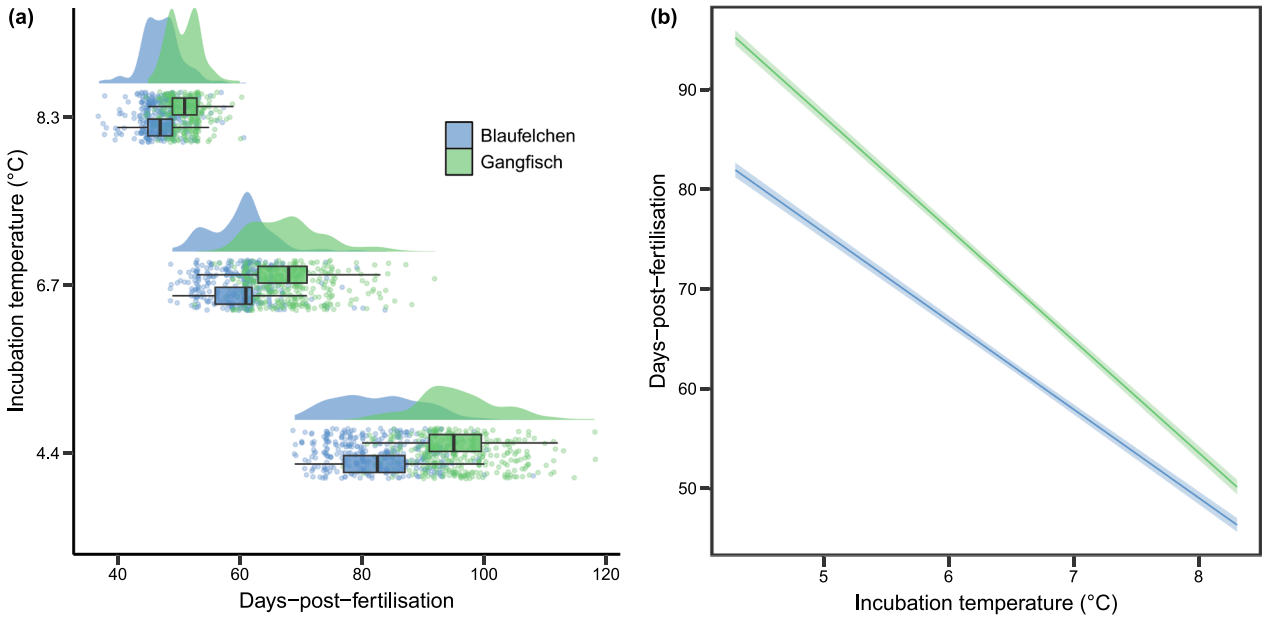

Fig. 1. Hatching dates (days-post-fertilisation) of Blaufelchen and Gangfisch. (a) Distribution of hatching dates (days-post-fertilisation) over the three different incubation temperature treatments. Half-violin plots show distribution of hatching dates throughout embryogenesis. Box plots show medians, quartiles and maximum and minimum values (excluding outliers). Circular markers show hatching dates of individual larvae (b) Predicted temperature–dependent values, with 95% confidence intervals, of mean hatch dates (shaded area: 95% CI) produced by linear mixed model of days-post-fertilisation hatching dates.

Table 2
Differences between average hatch dates of this study (incubated in microplates kept in climate chambers; and in incubation jars kept in a hatchery) and those based on a hatch model given in Eckmann, 1987. Hatch date values are reported in days–post–fertilisation (DPF). Statistically significant tests are highlighted in bold. Species = Fish species tested; Temp. = average incubation temperature; Median / mean hatch = median and mean hatch dates of data from our study; Eckmann median hatch date = median hatch date calculated using Eckmann's model values; *df* = degrees of freedom; *t* = t ratio value; *p* = *p*-value of *t*-test (alpha = <0.05).

Species	Temp. (°C)	Median / mean hatch (DPF)	Eckmann median hatch (DPF)	*df*	*t*	*p*
Chambers						
Blaufelchen	**4.4**	**83 / 83**	**67**	**341**	**39.17**	**<.0001**
Blaufelchen	**6.6**	**61 / 60**	**48**	**358**	**44.95**	**<.0001**
Blaufelchen	**8.3**	**47 / 47**	**37**	**352**	**61.53**	**<.0001**
Gangfisch	**4.3**	**95 / 96**	**77**	**346**	**50.97**	**<.0001**
Gangfisch	**6.6**	**68 / 68**	**54**	**327**	**41.59**	**<.0001**
Gangfisch	**8.3**	**51 / 51**	**41**	**275**	**61.1**	**<.0001**
Hatchery						
Blaufelchen	7.1	47 / 47	44	4	1.40	0.2337
Gangfisch	7.1	51 / 51	50	4	0.36	0.7395

3.3. At-hatch larval characteristics

Larval length-at-hatch had a negative, and yolk-sac volume a positive, relationship with temperature. Gangfisch length-at hatch was higher than Blaufelchen's, whilst Blaufelchen yolk-sac volumes were higher than Gangfisch's (Fig. 3). Species and incubation temperature significantly affected length-at-hatch and yolk-sac volume (Table 4).

Microscope inspection of spinal deformities yielded similar results to those of hatch deformities. Temperature and the interaction of species and temperature being statistically significant ($n = 691$, $R^2 = .085$, $p = <.0001$). Both species had very low probabilities of having a spinal deformity (< 1%) at historic incubation temperature, which increased to 10 % and 22 % for Blaufelchen and Gangfisch, respectively, at far–future temperature. No explanatory variables significantly affected 'other' hatch deformities ($n = 691$, $R^2 = .025$, $p = 0.357$).

3.4. Yolk sac absorption

Both incubation temperature and post-hatch rearing temperature impacted yolk-sac absorption time. Incubation temperature's relationship to yolk-sac absorption time was positive, and the post-hatch rearing temperature's negative (Fig. 3). The whole model explained 98 % of the variation of yolk-sac absorption dates ($R^2 = .98$, $F(5, 6) = 63.7$, $p = <.0001$). All explanatory variables except one were statistically significant (Table 4). Post-hatch rearing temperature had the largest effect on yolk-sac absorption dates, followed by incubation temperature, species, and the interaction between species and incubation temperature (Table 4). Yolk sacs of Blaufelchen incubated at far-future temperature and reared in the warmed tank treatment took 29 % longer to absorb than Gangfisch yolk sacs, but Blaufelchen yolk-sac absorption time lasted only 19 % longer than Gangfisch's in the lake water treatment (Fig. 3). Interspecific differences in yolk-sac absorption time were far lower in larvae incubated at historic temperature (Fig. 3).

3.5. Larval mortality

Average Gangfisch mortality (10 %) was significantly higher ($t(6) = -2.59$, $p = 0.0414$) than Blaufelchen mortality (6 %). The regression model explained most data variability ($R^2 = 0.92$, $F(5, 6) = 14.17$, $p = 0.0029$). The mortality in the warmed aquarium treatments was similar

Table 3
Results of least squares regressions for different sources of embryonic mortality in two species (Blaufelchen and Gangfisch) of coregonines. The response variable tested in the model is shown in italics and model effects are shown below it. Temperature is a continuous variable. Square-root transformed percentages of mortality types per microplate were the response variable values used in these analyses. Statistically significant model effects are highlighted in bold. Estimate = parameter estimate of model term coefficient; *SE* = standard error of parameter estimates; t = t ratio value (degrees of freedom, numerator degrees of freedom); η^2= effect size parameter, 0.01 indicates a small, 0.06 a medium and 0.14 a large effect; p = p-value of t-test (alpha = <0.05)

Models and model effects	Estimate	*SE*	t	η^2	p
'Fungal' infections					
Intercept	**−0.067**	**0.026**	**−2.52 (1, 104)**	–	**0.0131**
Species	−0.007	0.007	−1.00 (1, 104)	0.0086	0.3174
Incubation temperature	**0.013**	**0.004**	**3.43 (1, 104)**	**0.1001**	**0.0009**
Species*Incubation temperature	−0.004	0.004	−0.86 (1, 104)	0.0064	0.3891
Bacterial infections					
Intercept	**−2.471**	**0.044**	**−5.57 (1, 104)**	–	**<.0001**
Species	**−0.476**	**0.011**	**−4.32 (1, 104)**	**0.0847**	**<.0001**
Incubation temperature	**0.597**	**0.067**	**8.89 (1, 104)**	**0.3581**	**<.0001**
Species*Incubation temperature	**−0.292**	**0.067**	**−4.36 (1, 104)**	**0.0861**	**<.0001**
Developmental abnormalities					
Intercept	**4.763**	**0.378**	**12.60 (1, 104)**	–	**<.0001**
Species	**−0.195**	**0.094**	**−2.08 (1, 104)**	**0.0382**	**0.0399**
Incubation temperature	−0.104	0.057	−1.81 (1, 104)	0.0290	0.0728
Species*Incubation temperature	−0.072	0.057	−1.27 (1, 104)	0.0142	0.2082
Algal overgrowths					
Intercept	−0.200	0.013	−1.54 (1, 104)	–	0.1257
Species	−0.019	0.032	−0.59 (1, 104)	0.0032	0.5577
Incubation temperature	**0.040**	**0.020**	**2.05 (1, 104)**	**0.0384**	**0.0433**
Species*Incubation temperature	−0.013	0.020	−0.68 (1, 104)	0.0043	0.4968
Hatch deformities (% of hatched larvae)					
Intercept	−0.373	0.051	−0.73 (1, 104)	–	0.4693
Species	0.014	0.127	0.11 (1, 104)	0.0001	0.9148
Incubation temperature	**0.249**	**0.078**	**3.21 (1, 104)**	**0.0901**	**0.0018**
Species*Incubation temperature	−0.033	0.078	−0.42 (1, 104)	0.0015	0.6759
All embryonic mortality					
Intercept	**3.430**	**0.390**	**8.80 (1, 104)**	–	**<.0001**
Species	**−0.426**	**0.097**	**−4.41 (1, 104)**	**0.1312**	**<.0001**
Incubation temperature	**0.190**	**0.060**	**3.21 (1, 104)**	**0.0698**	**0.0017**
Species*Incubation temperature	**−0.223**	**0.060**	**−3.78 (1, 104)**	**0.0966**	**0.0003**
Total mortality					
Intercept	**3.346**	**0.371**	**9.01 (1, 104)**	–	**<.0001**
Species	**−0.393**	**0.092**	**−4.27 (1, 104)**	**0.1184**	**<.0001**
Incubation temperature	**0.245**	**0.056**	**4.36 (1, 104)**	**0.1236**	**<.0001**
Species*Incubation temperature	**−0.200**	**0.056**	**−3.56 (1, 104)**	**0.0823**	**0.0006**
Total mortality (excl. developmental abnormalities)					
Intercept	**−2.317**	**0.447**	**−5.18 (1, 104)**	–	**<.0001**
Species	**−0.333**	**0.111**	**−3.00 (1, 104)**	**0.0386**	**0.0034**
Incubation temperature	**0.705**	**0.068**	**10.40 (1, 104)**	**0.4654**	**<.0001**
Species*Incubation temperature	**−0.228**	**0.068**	**−3.37 (1, 104)**	**0.0488**	**0.0011**

in both species, varying from 10 % to 18 % (Fig. 4). Blaufelchen mortality in the lake water aquarium treatment was generally lower, at 1–4 %, whilst Gangfisch mortality varied between 5–9 % (Fig. 4 (a-c). Whereas Gangfisch mortality was positively related to incubation temperature, Blaufelchen mortality was negatively related to incubation temperature (Fig. 4 (b and c). The most important significant effects in the larval mortality model were (in order of effect size) post-hatch rearing temperature, the interaction of incubation temperature and species, followed by the species effect (Table 5).

3.6. Larval growth performance

Incubation and rearing temperature affected larval performance (Fig. 4; Table 5). Model certainty measures (R^2) varied from a low of 0.1 (for Thermal Growth Coefficient) to a high of 0.98 for Feed Conversion Efficiency. Regressions of larval growth and performance were always significant (p = <.0001).

Gangifsch Specific Growth Rate (SGR) values were higher than Blaufelchen SGR values. Gangfisch had a higher mean SGR^{Length} than Blaufelchen, and values of SGR^{Length} were higher at higher post-hatch rearing temperatures (Fig. 4 (d-f)). Blaufelchen SGR^{Length} values were related to incubation temperature, with higher incubation temperature resulting in higher SGR^{Length} in both aquarium treatments. This incubation temperature–dependent pattern was more pronounced in Blaufelchen. Blaufelchen larvae incubated at the warmest temperature had length growth rates 2 % higher than those of Gangfisch. But Blaufelchen incubated under the coolest temperature had SGR^{Length} values 4–6 % lower than those of Gangfisch (Fig. 4 (e and f)). Predicted values of SGR^{Weight} showed opposing interspecific incubation temperature-dependent relationships. Higher tank temperatures increased daily weight gain (Table 5). Again, the incubation temperature–dependent growth patterns were similar to those of daily length gain, with Gangfisch values being 0–2 % lower than for Blaufelchen larvae incubated at far–future temperature. For larvae incubated at the coolest temperature, Gangfisch's daily weight gain was 7 % higher than Blaufelchen's daily weight gain (Fig. 4 (h and i)).

Thermal Growth Coefficient (TGC) response to temperature was mostly influenced by species and the interaction between species and incubation temperature (Table 5). The Gangfisch TGC grand marginal mean was higher, at 0.55, than that of Blaufelchen, at 0.52 (t(354) = -3.69, p = 0.0003). Gangfisch TCG values were either the same or slightly higher at higher water temperatures (Fig. 4 (j-l)). Blaufelchen differed from Gangfisch in their reaction to post-hatch rearing temperature as higher rearing temperature negatively affected TGC values of Blaufelchen but not of Gangfisch (Fig. 4 (k and l)). Gangfisch and Blaufelchen TCG values did not vary from one another by more than 5 % in larvae incubated at far–future temperature. But, Gangfisch larvae incubated under historic temperature exhibited TGC values 10–13 %

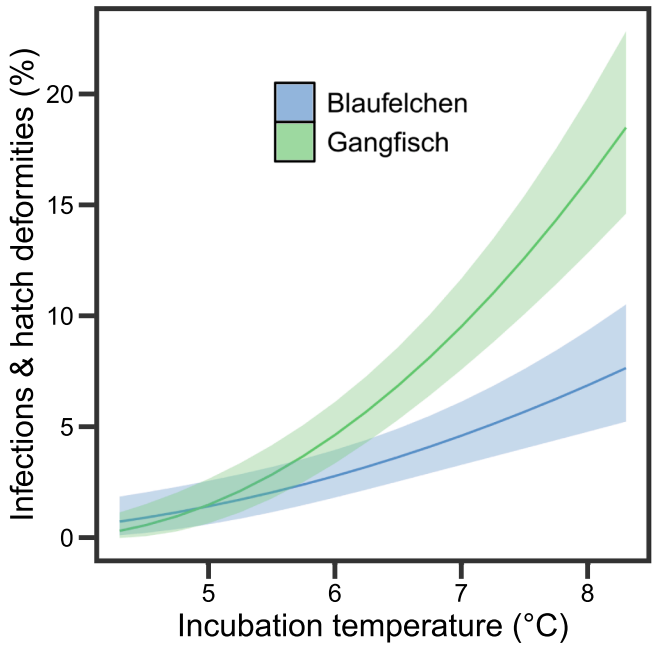

Fig. 2. Embryonic mortality of Blaufelchen and Gangfisch. Predicted temperature–dependent mortality values (shaded area: 95% CI) produced by least-squares regression of 'infections and hatch deformities'. This includes all types of embryonic mortality, excluding developmental abnormalities, i.e. 'fungal' infections, bacterial infections, algal overgrowths and hatch deformities (as a percentage of total embryos).

higher than those of Blaufelchen incubated at the same temperature (Fig. 4 (k and l)).

Both species exhibited higher Food Conversion Efficiency (FC) values at higher post-hatch rearing temperatures. Blaufelchen FC from all incubation treatments was similar in lake water, but in warmed water FC values were positively related to incubation temperature (Fig. 4 (n)). The effect of incubation temperature on FC was reversed in Gangfisch: this trend was stronger in Gangfisch and present in larvae reared in lake and warmed water (Fig. 4 (o)). However, rearing temperature had a far larger effect on FC ($\eta^2 = 0.61$) than the interaction between species and incubation temperature did ($\eta^2 = 0.17$) (Table 5), with Blaufelchen FC increasing by an average of 30 % between lake and warmed rearing temperatures and in Gangfisch by an average of 34 % between the lake and warmed rearing tanks (Fig. 4. (n and o)).

3.7. *Historic and future phenologies of Upper lake Constance coregonines*

Between 1966 and 2022, ULC's average water temperatures have risen substantially. During this time, water temperatures at 100 and 250 m depth have risen by 0.6 °C; at 20 m depth, water temperatures have risen by around 1.4 °C. In the same period, surface water temperature has risen by around 1.2 °C. Winter water temperatures in ULC were predicted to rise moderately or more substantially, from the early (2011–2040) to late (2071–2100) 21st century, depending on the Shared Socioeconomic Pathway (ssp) used to project air temperature. Under ssp370 and ssp585 water temperature at 20 m depth increased from 7.1 °C in the early 21st century under both scenarios, to 8.4 °C under ssp370 and 8.6 °C under ssp585 in the late 21st century. At 250 m depth, water temperatures were predicted to increase from 4.9 °C to 5.4 °C from the early to late 21st century under ssp370, and from 4.7 °C to 5.6 °C under ssp585. Under the low–emission ssp126 scenario, water temperatures were predicted to never rise by more than 0.4 °C between the early and mid-21st century (2041–2070), before falling again during the late 21st century. More information on temperature predictions is given in Appendix S1.

The future predictions of the average time until yolk-sac absorption varied depending on species, depth and the ssp used. Here, we compare the differences in predicted time (post-fertilisation) until yolk-sac absorption between the early, mid and late 21st century, based on our predicted water temperatures. Following ssp126, time to yolk sac absorption for Gangfisch embryos spawned at 20 m depth advanced four days (90 to 86 days) between the early and mid-21st century (Fig. 5 (a)). However, the time until yolk sac absorption increased to 88 days in the late 21st century. Following the most carbon–intensive ssp (ssp585), shallow–spawning Gangfisch yolk-sac absorption times advanced by 21 days (89 to 68 days) between the early and late 21st century. For Gangfisch spawning at 100 m depth, yolk-sac absorption times were reduced by a maximum of two days under ssp126 and 17 days under ssp585 (Fig. 5. (c)). Future predicted Blaufelchen yolk-sac absorption times only reduced by a maximum of two days within the 21st century, based on the temperature predictions following ssp126. Following ssp370 (Fig. 5 (b)), Blaufelchen yolk-sac absorption time advanced by seven days for shallower spawning (100 m) Blaufelchen and six days for deeper (250 m) spawning Blaufelchen. The most extreme advances of time to full yolk-sac absorption of Blaufelchen occurred following ssp585. For Blaufelchen embryos spawned at 100 m and 250 m depth, time to yolk sac absorption was shortened by 12 and 11 days, respectively, between the early and late 21st century (Fig. 5 (c)).

Based on historical data, the average time (both species, all depths) until yolk sac absorption advanced by five days (113 to 105) between 1966–1975 and 2006–2015. Yet, during 2016–2022 yolk sac absorption time dropped to 100 days, resulting in a total average advancement of 13 days between the beginning and end of the dataset (Fig. 5 (d)). Time until Blaufelchen yolk sac absorption has advanced 9 % during the period of this dataset, decreasing from 108 to 96 days for Blaufelchen spawned at 100 m depth and from 109 to 100 days for deeper-spawning Blaufelchen. In the same period, Gangfisch yolk sac absorption dates have advanced by 13–19 %. Deeper-spawned Gangfisch average yolk sac absorption times went from 120 to 105 days between 1966 and 1975 and 2016–2022. During the same time, shallower-spawning Gangfisch yolk sac absorption time advanced by 21 days (112 to 91) (Fig. 5 (d)).

4. Discussion

This study adds to the considerable wealth of research exploring the potential consequences of ongoing climate change on the survival and development of coregonines during embryogenesis and early larval life. In line with general expectations, temperature fundamentally affected the survival and phenology of coldwater, stenothermic coregonine larvae, raising concern about direct and indirect negative climate change impacts on the recruitment of the already dwindling ULC coregonine stocks. Subtle differences in the responses to higher temperatures between the two coregonine species included in this study suggest species–specific effects, highlighting the need for species-specific climate change risk assessments.

In our study, Blaufelchen and Gangfisch embryogenesis consistently lasted longer than in Eckmann (1987), which is presumably driven by differences in methodology, with our study probably approximating realistic deep-water, lake-bottom conditions more closely (see arguments below). The hatching model terms from Eckmann (1987) have already been used to predict how climate warming could alter coregonine phenology in ULC (Straile et al., 2015; Stewart, 2022). Using a model which accurately predicts hatching dates in a natural setting is paramount when studying temperature–dependent phenology. The hatch dates we recorded differed from those predicted by Eckmann's model by 10 days at the highest incubation temperature tested and up to 18 days at the lowest incubation temperature. These large differences are quite relevant if one aims to predict hatching phenology. Thus, our study shows how different hatching time models, and the methodologies that produce them, can lead to wholly different inferences on the potential ecological consequences of climate change.

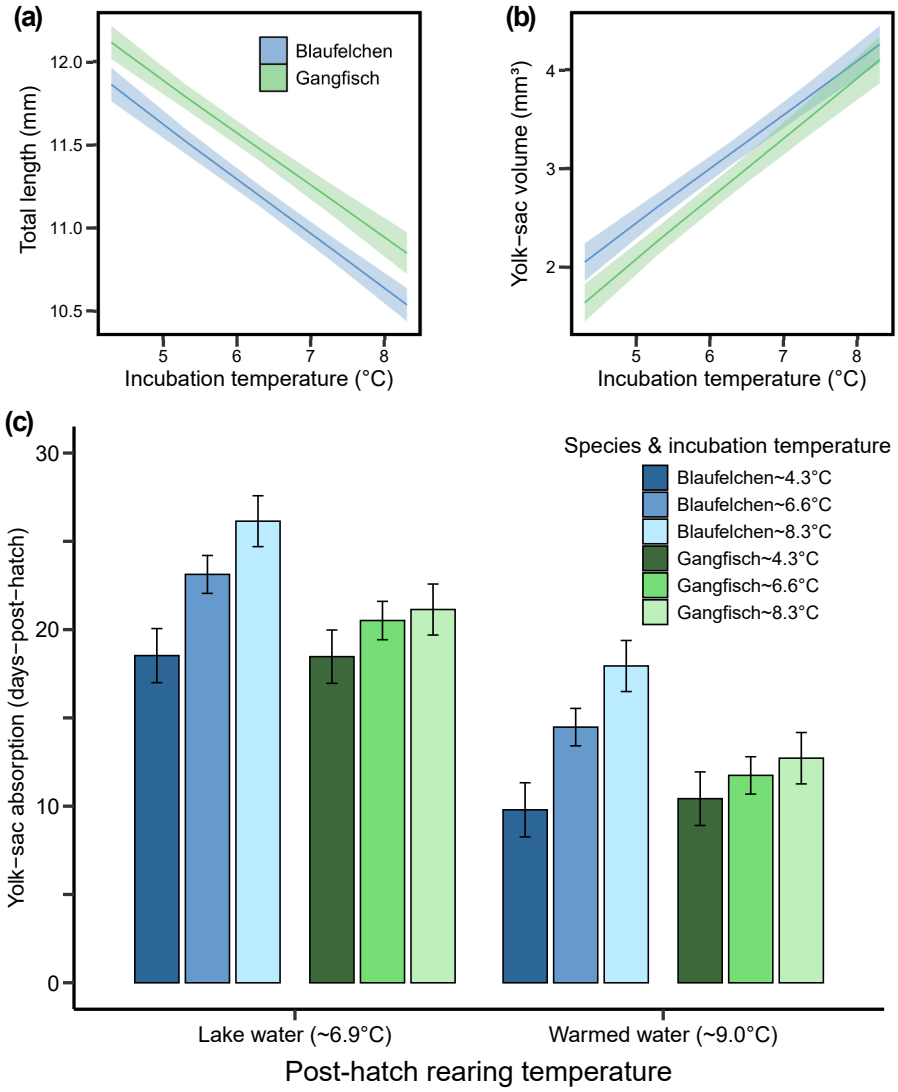

Fig. 3. At-hatch larval measurements and yolk-sac absorption times of Blaufelchen and Gangfisch, based on results of least-squares regression models (a) Temperature-dependent hatch size (shaded area: 95% CI) (b) Temperature-dependent yolk-sac volume at-hatch (shaded area: 95% CI) (c) Temperature-dependent duration until full yolk-sac absorption (error bars: 95% CI) for larvae taken from all incubation temperature treatments, which were reared under two post-hatch rearing temperature regimes.

Though the hatching dates recorded in our main experiment differed significantly from the results of Eckmann (1987), hatching dates that we recorded in incubation jars kept at Langenargen hatchery did not differ from those predicted by Eckmann's hatching model. In Eckmann's experiment, embryos were kept in incubation jars, constantly agitated by the aeration apparatus, and were illuminated for 12 hours per day. These conditions resemble those in the incubation jars from our experiment, as embryos experienced constant mechanical agitation and were illuminated with natural and artificial light. This is quite different to the natural situation, where most embryos lie motionless and in darkness, on the lake floor. Other studies of coregonine embryogenesis have found that both illumination and mechanical agitation induced early hatching (John and Hasler, 1956; Næsje et al., 1995; Næsje and Jonsson, 1988). Other species of non-salmonid fish, such as walleye (*Sander vitreus*), have also been shown to hatch earlier in flow-through incubation systems than in static incubation systems (Johnston et al., 2021). Salmonid incubation times can be accelerated at higher flow rates due to increased higher dissolved O_2 (Ciuhandu et al., 2007; Miller et al., 2008; Wood et al., 2019). Though dissolved O_2 in ULC may be higher than in microplates where no water exchange occurs, hypoxia of bottom water layers was, but is no longer, a major issue in ULC (Braum and Quos, 1981; Wahl and Löffler, 2009), therefore, the conditions in microplates may more accurately simulate O_2 conditions experienced by ULC coregonine embryos than those that occur in incubation jars. Unfortunately, we did not record O_2 in our experiment, so we cannot directly determine the effect of O_2 concentrations as they relate to our results. Further studies on the likely synergistic effects of incubation technique, O_2 concentrations and mechanical disturbance could help elucidate which factors most heavily influence hatching dates. Further analysis of which current model more accurately predicts wild coregonine hatching, using temporal data of wild larval densities and hatch dates in ULC, may reveal which incubation method best replicates natural hatching times. For the time being, based on the rationale outlined above, we feel that our experimental setup better approximated realistic conditions.

The results of our embryogenesis study suggest that future warming could directly reduce coregonine recruitment in ULC by increasing embryo mortality. However, Gangfisch embryonic mortality exceeding Blaufelchen's at higher temperatures was unexpected because, in

Table 4
Results of least-squares regressions on at-hatch larval morphometrics and yolk sac absorption times of two species of larval coregonines (Blaufelchen and Gangfisch). The response variable tested in the model is shown in italics and model effects are shown below it. Temperature (incubation and post-hatch rearing) is a continuous variable. For models of at–hatch larval measurements, the unit of replication used was an individual larva. The model of yolk-sac absorption used the measured time until yolk-sac absorption in an individual aquarium as the response variable. Statistically significant model effects are highlighted in bold. Estimate = parameter estimate of model term coefficient; *SE* = standard error of parameter estimates; $t = t$ ratio value (degrees of freedom, numerator degrees of freedom); η^2 = effect size, 0.01 indicates a small, 0.06 a medium and 0.14 a large effect; $p = p$-value of t-test (alpha = <0.05).

Models and model effects	Estimate	*SE*	*t*	η^2	*p*
Length-at-hatch					
Intercept	**13.381**	**0.094**	**142.32 (1, 687)**	–	**<.0001**
Species	**−0.014**	**0.024**	**−5.77 (1, 687)**	**0.0268**	**<.0001**
Incubation temperature	**−0.032**	**0.015**	**−21.76 (1, 687)**	**0.3811**	**<.0001**
Species*Incubation temperature	−0.007	0.015	−0.48 (1, 687)	0.0002	0.6314
Yolk-sac volume					
Intercept	**−0.661**	**0.177**	**−3.72 (1, 687)**	–	**0.0002**
Species	**0.147**	**0.046**	**3.20 (1, 687)**	**0.0089**	**0.0014**
Incubation temperature	**0.583**	**0.028**	**20.76 (1, 687)**	**0.3735**	**<.0001**
Species*Incubation temperature	−0.032	0.028	−1.13 (1, 687)	0.0011	0.2576
Yolk-sac absorption					
Intercept	**35.798**	**2.126**	**16.84 (1, 6)**	–	**<.0001**
Species	**1.250**	**0.282**	**4.44 (1, 6)**	**0.0607**	**0.0044**
Incubation temperature	**1.320**	**0.172**	**7.68 (1, 6)**	**0.1816**	**0.0003**
Post-hatch rearing temperature	**−3.527**	**0.234**	**−15.04 (1, 6)**	**0.6970**	**<.0001**
Species*Incubation temperature	**0.742**	**0.172**	**4.32 (1, 6)**	**0.0575**	**0.0050**
Species*Post-hatch rearing temp.	−0.067	0.234	−0.29 (1, 6)	0.0003	0.7852

nature, Gangfisch embryos are more likely to experience higher temperatures than Blaufelchen embryos. Therefore, one would expect that Gangfisch embryos would be less sensitive to temperature. In a study by Eckmann (2015) Gangfisch embryos did experience higher rates of later–stage embryonic mortality than Blaufelchen, as in our study. Parentage could account for this interspecific mortality difference (Eckmann, 2015; Stewart et al., 2021) but was not investigated in our study. Higher early–stage mortality can be caused by reduced fertilisation success at higher temperatures (Cigni et al., 2010), though the results of our study do not fit this pattern. But our study does suggest that cooler incubation temperatures reduce late–stage mortality (Bloomer et al., 2023) by reducing the prevalence of bacterial infections. Research on how temperature impacts mortality at different stages of embryonic development, and whether interspecific differences in mortality observed in our study remain interannually consistent between cohorts, are necessary to more fully understand the impacts of future warming on ULC coregonines.

Hatching windows also decreased strikingly with temperature and showed increasing interspecific overlap, which may reduce the chance of larvae hatching when suitable food is available and increase interspecific competition for prey. Blaufelchen and Gangfisch embryos (if laid simultaneously) experience overlapping hatching dates at lower temperatures, but the amount of overlap increases with temperature. At lower temperatures, if one species' hatch window does not coincide with suitable resource densities, there is a chance the other sympatric species' larvae could experience a good phenological match with food resources. It may be that differences in the hatching times of ULC coregonines evolved as a compensatory measure which reduces competition between Blaufelchen and Gangfisch larvae (Johansson et al., 2015). At higher temperatures, however, the chances of phenological asynchronies between larvae and prey arising in both species become more likely (Fig. 6). As a result, competition between sympatric coregonine larvae might increase, and recruitment of one or both species may be negatively affected as a result of increasing phenological overlap (Arzel et al., 2014; Krabbenhoft et al., 2014; Dong et al., 2023).

Although peak spawning of Blaufelchen and Gangfisch tends to occur simultaneously, in early December, the spawning period of Gangfisch can last several weeks. As Blaufelchen eggs settle in the deepest parts of the lake, where temperatures are far more stable throughout winter (Sommer, 1985; Peeters et al., 2007), and the fact that Blaufelchen tend to spawn within a short time window (Hirsch et al., 2013; Rey et al., 2023), means that changes in within-season winter air temperature will probably have little impact on embryogenesis. However, the mean spawning date of Blaufelchen may indeed occur later in the year as water temperatures increase (Wahl and Löffler, 2009), but even under higher-carbon-emission scenarios, it is unlikely that the mean spawning date of Blaufelchen will be delayed by more than a week by the end of the 21st century (Stewart, 2022). Gangfisch can spawn as early as mid-November until as late as January (Hirsch et al., 2013; Rey et al., 2023). Temperatures in shallower water (20 m depth) during November regularly exceed 10 °C, before falling to between ~ 7–10 °C in early December, then dropping to under 7 °C (until May) after mid-December. Gangfisch that spawn earlier would produce embryos which experience higher average temperatures than later spawning Gangfisch, resulting in reduced incubation periods for those earlier-spawned embryos and possibly higher mortality rates. It is likely that Gangfisch larvae which hatch very early (for example, in January) may struggle to find suitable densities of zooplankton prey, though slower growth rates in lower temperatures may allow earlier-hatching larvae to better cope with lower zooplankton densities. The timing of Gangfisch spawning is an understudied subject and further investigation may elucidate how changing late-autumn and winter temperatures will impact embryos produced by earlier and later-spawning Gangfisch differentially.

A caveat of our study is that parent fishes were only sampled on one day, and not throughout the spawning season. Because Blaufelchen tend to spawn within a short time window, secondary impacts of spawning time on embryogenesis and larval growth are probably minimal. In the case of Gangfisch, though, spawning time may be a more consequential issue because the spawning period of this species is longer. Coregonines that spawn over longer time periods may, depending on when they spawn, allocate differing amounts of energy to either egg quality or fecundity, resulting in differences in the mass and chemical composition of eggs (Lahti and Muje, 1991). The relative investment of a parent female fish into either higher egg quality or higher fecundity can result in differences in the mortality rates of their offspring (Karjalainen et al., 2016). Embryogenesis and larval growth experiments that examine spawning time's impact on drivers of population dynamics, including mortality and growth, may yield interesting results. If earlier or later spawning Gangfisch produce offspring that exhibit traits that make them more or less likely to survive, then it may be that earlier or later spawning individuals are more important to overall population recruitment. Alternatively, intraspecific variation of spawning time could simply be a 'bet-hedging' strategy. Such a strategy could potentially increase the survival rate of at least a portion of a year class via

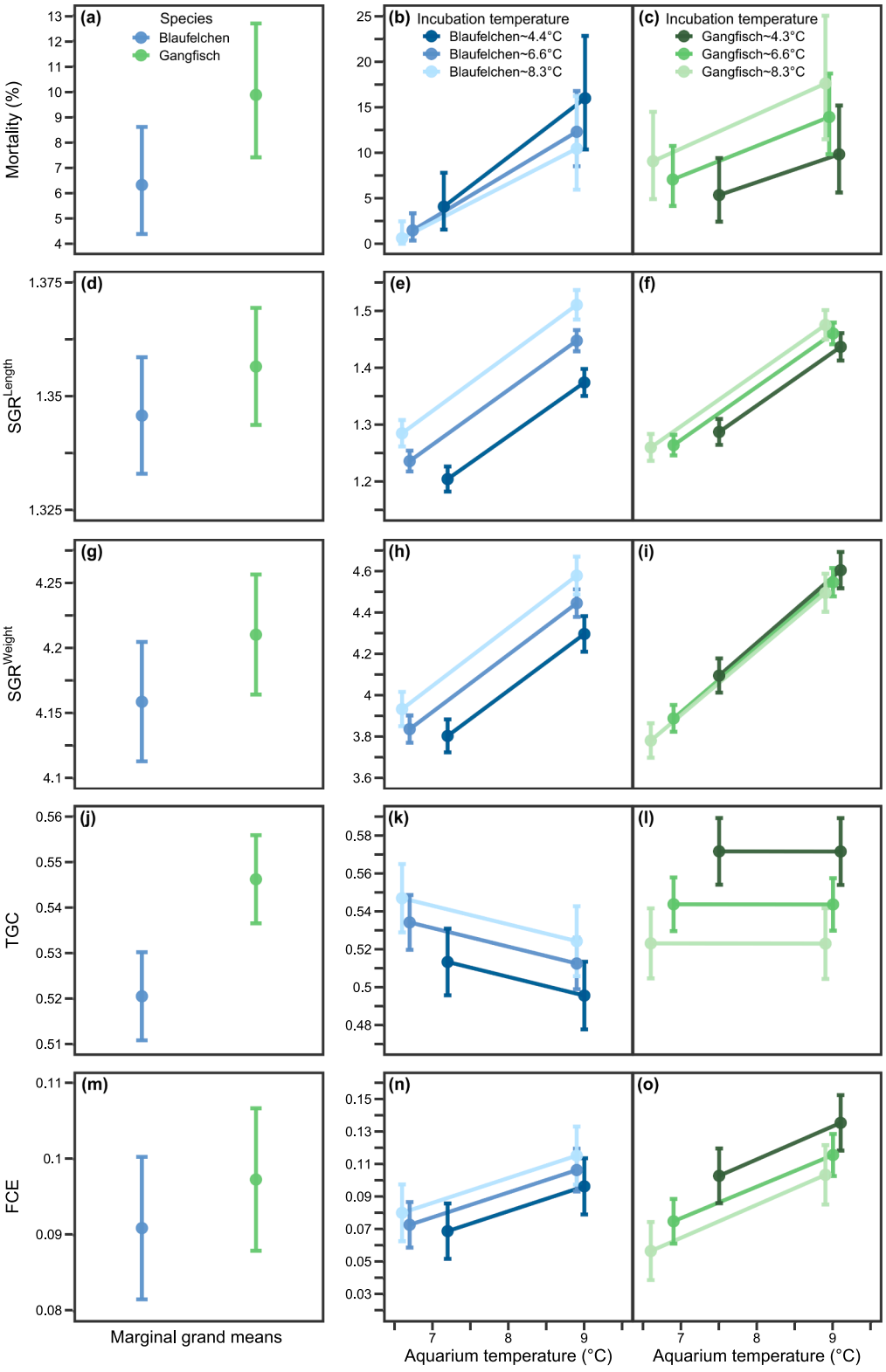

Fig. 4. Grand marginal means and incubation-temperature specific predicted values (error bars: 95% CI) of larval mortality and various measures of growth and performance for Blaufelchen and Gangfisch raised under two rearing temperature regimes. Each row of plots, from left to right, show grand marginal means of Blaufelchen and Gangfisch, then predicted values of Blaufelchen from all incubation temperature treatments, followed by predicted values of Gangfisch from all incubation temperature treatments. All values were derived from least-squares regressions. Performance parameters shown are (a), (b) and (c) larval mortality; (d), (e) and (f) Specific Growth Rate of length; (g), (h) and (i); Specific Growth Rate of weight; (j), (k) and (l) Thermal Growth Coefficient; (m), (n) and (o) Feed Conversion Efficiency.

Table 5
Least-squares regression results of larval mortality, larval growth and larval performance measures for two species of larval coregonines (Blaufelchen and Gangfisch). The response variable tested in the model is shown in italics and model effects are shown below it. Temperature (incubation and post-hatch rearing) is a continuous variable. A single percentage value of larval mortality (square-root transformed for analysis) per aquarium was calculated and used as the response variable in the mortality model. Most other models used the measurements and calculated growth/performance values of individuals as response variable values: from a sample of 30 larvae, taken from each aquarium. For the Feed Conversion Efficiency Ratio model, a single response variable value of feed conversion efficiency per aquarium was calculated. Statistically significant model effects are highlighted in bold. Estimate = parameter estimate of model term coefficient; *SE* = standard error of parameter estimates; t = t ratio value (degrees of freedom, numerator degrees of freedom); η^2 = effect size, 0.01 indicates a small, 0.06 a medium and 0.14 a large effect; p = p-value of t-test (alpha = <0.05).

Models and model effects	Estimate	*SE*	t	η^2	p
Mortality (%)					
Intercept	**−3.863**	**1.134**	**−3.41 (1, 6)**	–	**0.0144**
Species	**−0.314**	**0.121**	**−2.59 (1, 6)**	**0.0871**	**0.0414**
Incubation temperature	0.064	0.075	0.85 (1, 6)	0.0093	0.4304
Post-hatch rearing temperature	**0.792**	**0.118**	**6.69 (1, 6)**	**0.5821**	**0.0005**
Species*Incubation temperature	**−0.224**	**0.075**	**−2.99 (1, 6)**	**0.1160**	**0.0245**
Species*Post-hatch rearing temp.	0.270	0.118	2.28 (1, 6)	0.0678	0.0626
Specific Growth Rate^{Length} (%/-d)					
Intercept	**0.772**	**0.018**	**41.91 (1, 354)**	–	**<.0001**
Species	−0.002	0.002	−1.17 (1, 354)	0.0016	0.2440
Incubation temperature	**0.011**	**0.001**	**8.56 (1, 354)**	**0.0853**	**<.0001**
Post-hatch rearing temperature	**0.041**	**0.002**	**21.28 (1, 354)**	**0.5269**	**<.0001**
Species*Incubation temperature	**0.005**	**0.001**	**3.72 (1, 354)**	**0.0161**	**0.0002**
Species*Post-hatch rearing temp.	0.001	0.002	0.39 (1, 354)	0.0002	0.6988
Specific Growth Rate^{Weight} (%/-d)					
Intercept	**1.424**	**0.038**	**37.91 (1, 354)**	–	**<.0001**
Species	−0.006	0.004	−1.56 (1, 354)	0.0033	0.1202
Incubation temperature	**0.008**	**0.003**	**3.13 (1, 354)**	**0.0135**	**0.0019**
Post-hatch rearing temperature	**0.072**	**0.004**	**18.46 (1, 354)**	**0.4681**	**<.0001**
Species*Incubation temperature	**0.010**	**0.003**	**4.16 (1, 354)**	**0.0237**	**<.0001**
Species*Post-hatch rearing temp.	−0.004	0.004	−1.06 (1, 354)	0.0016	0.2880
Thermal Growth Coefficient					
Intercept	**0.589**	**0.032**	**18.20 (1, 354)**	–	**<.0001**
Species	**−0.013**	**0.003**	**−3.69 (1, 354)**	**0.0346**	**0.0003**
Incubation temperature	−0.003	0.002	−1.20 (1, 354)	0.0036	0.2320
Post-hatch rearing temperature	−0.005	0.003	−1.47 (1, 354)	0.0055	0.1421
Species*Incubation temperature	**0.010**	**0.002**	**4.38 (1, 354)**	**0.0486**	**<.0001**
Species*Post-hatch rearing temp.	−0.005	0.003	−1.46 (1, 354)	0.0054	0.1462
Feed Conversion Efficiency Ratio					
Intercept	−0.041	0.025	−1.61 (1, 6)	–	0.1588
Species	−0.003	0.003	−1.18 (1, 6)	0.0188	0.2828
Incubation temperature	−0.001	0.002	−0.55 (1, 6)	0.0042	0.5991
Post-hatch rearing temperature	**0.018**	**0.003**	**6.74 (1, 6)**	**0.6126**	**0.0005**
Species*Incubation temperature	**0.006**	**0.002**	**3.59 (1, 6)**	**0.1736**	**0.0115**
Species*Post-hatch rearing temp.	−0.003	0.003	−0.96 (1, 6)	0.0124	0.3753

mechanisms such as better synchronisation of larvae with prey resources or spatiotemporal avoidance of predators (Dolan et al., 2021; Otterson and Holt, 2023).

The impact of incubation temperature on at-hatch larval morphometrics was consistent with the findings of other studies (Lim et al., 2017; Mitz et al., 2019; Stewart et al., 2021). However, warmer water temperatures may override the starvation buffer conferred by the larger yolk–sacs of earlier-hatching larvae by accelerating yolk-sac absorption (Fig. 6). The ability to hatch at non-fixed stages of development may be an adaptation to synchronise larval hatching with resource abundance (Mitz et al., 2019). Yet, earlier–hatching fish larvae are smaller and more vulnerable to predation, perhaps outweighing the benefit of early hatching (Bailey, 1984; Garrido et al., 2015; Stige et al., 2019). Yolk-sac volumes were larger in earlier–hatching larvae, resulting in a longer period of endogenous feeding; but the temperature of the water at which larvae were reared had a stronger effect on yolk-sac absorption times. Blaufelchen yolk-sac absorption times lasted longer than Gangfisch's, which may be related to differences in Blaufelchen and Gangfisch spawning ecology. Blaufelchen normally hatch further away from the shore than Gangfisch, and might take longer to reach nursery habitats. The capacity of larvae to reach suitable nursery habitats could be an important driver of year–class strength (McKenna et al., 2008; McKenna and Johnson, 2009). Thus, larger, longer-lasting yolk sacs could have been selected for in Blaufelchen but because Gangfisch larvae probably take less time to reach nurseries, the selection pressure for a longer endogenous feeding period could be lower.

Larval mortality, growth and performance were modulated by incubation and rearing temperature, with potentially negative implications for larval recruitment under future warming. The reactions of each species to temperature differed somewhat. The pattern of incubation temperature-dependent Gangfisch mortality we found mirrors that found in a recent study of *Coregonus artedi*, but the incubation temperature–dependent reaction of Blaufelchen does not (Stewart et al., 2022). However, higher rearing temperatures had a negative effect on larval survival in our study, mirroring results from other studies of larval coregonines (Luczynski, 1991; Mahlzahn et al. 2003; Stejskal et al., 2021). A previous study of ULC coregonines showed that larval growth rates differed interspecifically and interannually between cohorts (Goebel et al., 2021). In our study, when observing only daily growth rates, Blaufelchen and Gangfisch showed similar temperature-dependent patterns: higher rearing temperatures resulted in higher growth rates. Thermal Growth Coefficient and Feed Conversion measures revealed subtler incubation and rearing temperature interactions. Larval Thermal Growth Coefficient values infer two points. Firstly, larval growth rates are related to incubation temperature, and the relationship between incubation temperature and growth differs between species. Secondly, lower incubation temperatures resulted in higher growth rates in Blaufelchen, but in Gangfisch, rearing temperature had no significant effect on growth. Feed Conversion Efficiency was higher at higher post-hatch rearing temperature in both species.

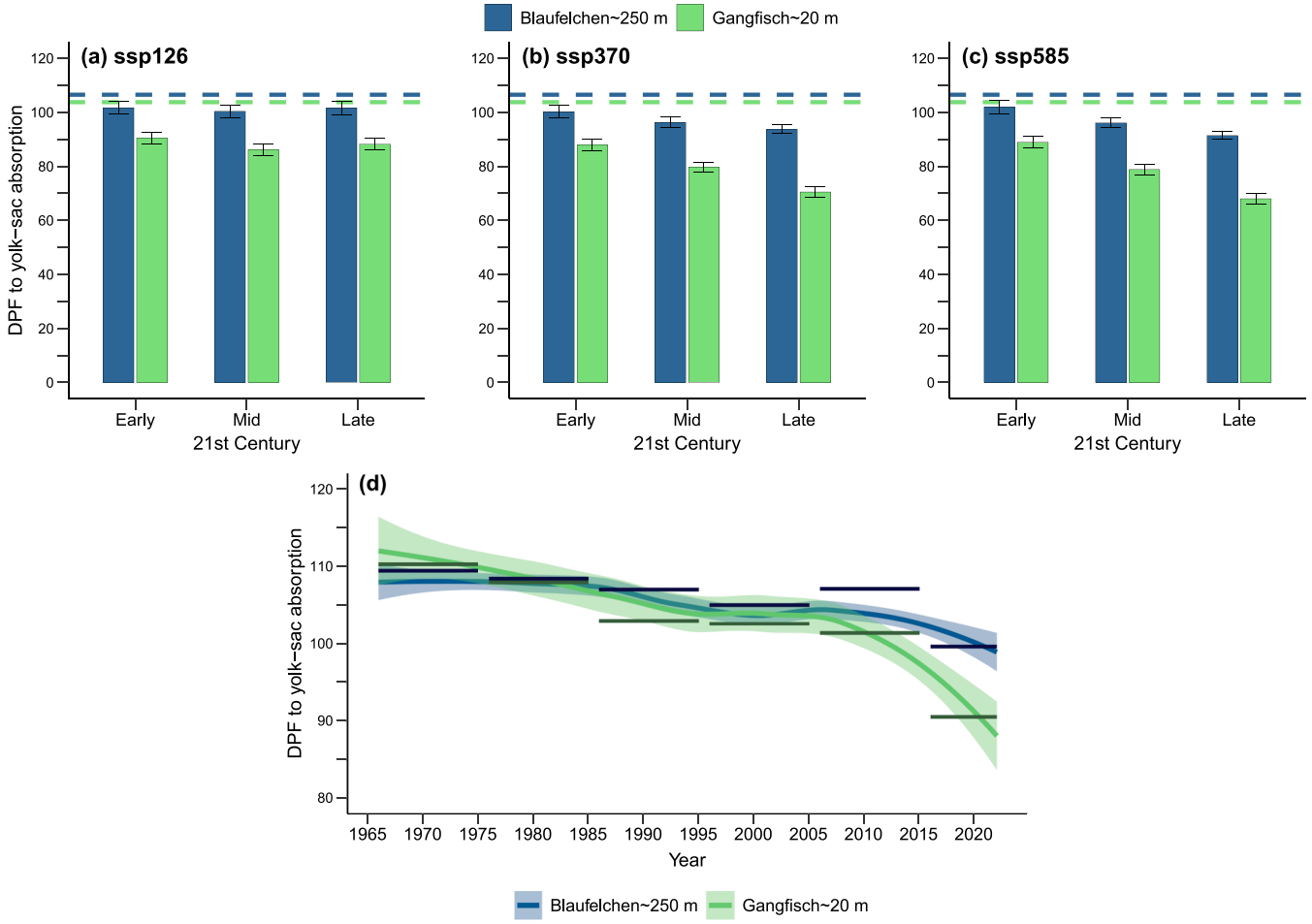

Fig. 5. Predicted future, following three different Shared Socioeconomic Pathways (ssp), and historic yolk-sac absorption times at the most ecologically-relevant spawning depths for Blaufelchen (250 m) and Gangfisch (20 m). (a) Average days post fertilisation (DPF) until full yolk-sac absorption in the early (2011 2040), mid (2041–2070) and late (2071–2100) 21st century, based on future temperatures predicted under ssp126. (b) Average DPF until full yolk-sac absorption in the early, mid and late 21st century, based on future temperatures predicted under ssp370. (c) Average DPF until full yolk-sac absorption in the early, mid and late 21st century, based on future temperatures predicted under ssp585. Dotted lines show average predicted yolk-sac absorption times (based on average water temperatures) for Blaufelchen (blue) and Gangfisch (green) during the period 1981–2010, which was the reference time period used to predict future air temperatures. (d) Predicted annual values of time (DPF) until full yolk-sac absorption based on historical Upper Lake Constance temperatures from 1966 to 2022. A Loess smoothing method was applied to the yolk-sac absorption time values. Different colours represent species and their spawning depths. Horizontal lines show decadal averages of time until yolk-sac absorption for Blaufelchen (dark blue) and Gangfisch (dark green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Incubation temperature–dependent Feed Conversion Efficiency was also observed. Though, similarly to the pattern observed with Thermal Growth Coefficient values, the species differed in their response to incubation temperature. Blaufelchen Feed Conversion Efficiency had a positive relationship with temperature, contrastingly, Gangfisch Feed Conversion Efficiency exhibited a negative relationship with incubation temperature. Another alpine *Coregonus* spp. embryogenesis and larval growth study (Steinbacher et al., 2017) also found that incubation temperature can determine growth and physiological characteristics until at least 81 days post-hatch. Our findings reveal that the thermal experience of ULC coregonines during embryogenesis continues to influence larval biology for months after hatching. Future warming might reduce larval recruitment by increasing larval mortality in Lake Constance. Furthermore, the longer–term impacts of incubation and rearing temperature on growth are of ecological relevance as it may mean that species–specific reaction norms result in each species' larval physiology responding differentially to changing temperatures (Fig. 6). Results from this study should be used to model the reality of how larval growth occurs in ULC, as has been done for other fish species (Fiksen and Reglero, 2022), and thus help develop a mechanistic understanding of how the interplay between larval growth and phenology affect larval recruitment in the natural setting.

Our predictions of future coregonine phenologies in ULC stress that the magnitude of climate change determines the magnitude of phenological change. Under ssp126, a 'green future' scenario in which tipping points are avoided and the criteria of the Paris Agreement can be achieved, phenologies could remain fairly stable throughout the 21st century. Unfortunately, humanity has set a course that is more on track towards the 'business-as-usual' scenario (ssp370), characterised by inadequate climate mitigation policies and the crossing of tipping points. Even the 'fossil fuel–intensive', worst-case scenario ssp585 might become a bitter reality (Raftery et al., 2017; Hausfather and Peters, 2020; Kemp et al., 2022). Under these more realistic, carbon-intensive scenarios, the date when larval coregonines begin to require exogenous nutrition might advance by one to two weeks by the end of the century. Perhaps more alarming and pertinent to the current fisheries situation in the lake is that the average time until full yolk-sac absorption may have already advanced 15 days between the periods of 1966–1975 and 2015–2022. Yet evidence suggests that zooplankton phenologies in ULC are also advancing. The timing of the chlorophyll

and *Daphnia* maxima in ULC already seems to have advanced by around two weeks between the 1980s and early 2000s (Straile et al., 2012), whilst a study of the copepod *Cyclops vicinus* in ULC suggests that earlier phytoplankton blooms lead to higher naupliar and copepodite survival (Seebens et al., 2009). In Lake Geneva, advancing *Daphnia* maxima may have resulted in a better phenological match between coregonine larvae and prey (Anneville et al., 2009). Though such positive situations may occur, evidence suggests future warming is more likely to lead to phenological asynchronisation between trophic levels. Studies indicate that warming leads to a lower abundance and sizes of zooplankton (Pothovern and Vanderploeg, 2022; Suchy et al., 2022; O'Connor et al., 2023). As the energetic demands of larval coregonines increase with water temperature, lower overall densities of zooplankton might increase the probability of larvae not synchronising with sufficient plankton densities (Fig. 6). Declining zooplankton size may also negatively impact coregonine populations, as recruitment may also rely on a good phenological match with zooplankton of the correct size (Crowder et al., 1987; Huebert and Peck, 2014; Hauss et al., 2023). Furthermore, larval coregonines develop in littoral nursery habitats, and zooplankton phenological shifts may occur years earlier in littoral areas

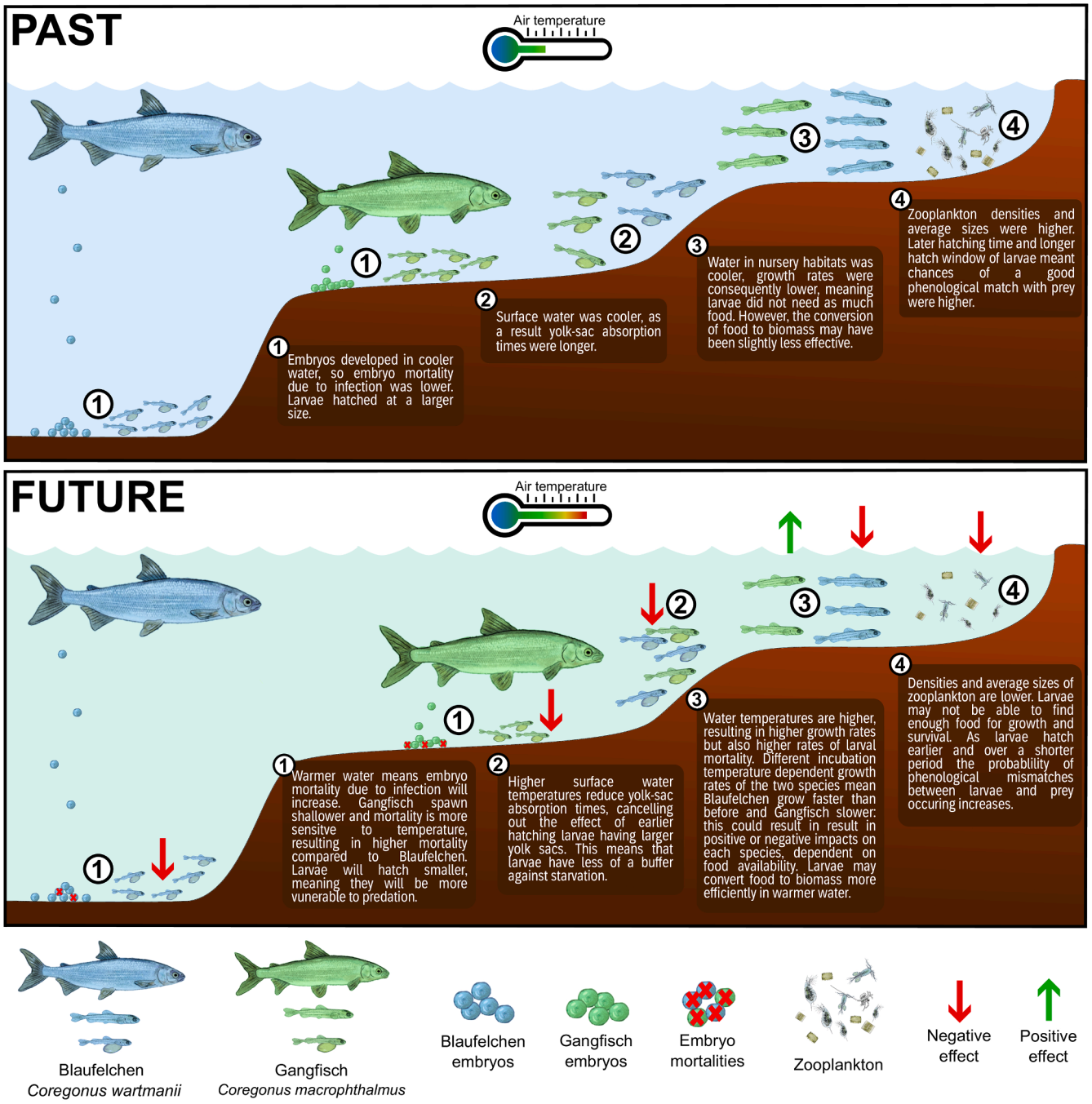

Fig. 6. Comparison of how cooler past temperatures and predicted warmer future temperatures could impact the early life history of coregonine populations in Upper Lake Constance, with additional reference as to how interspecific heterogeneity in temperature reaction norms could impact Blaufelchen and Gangfisch differentially. Numbers represent successive stages of early life, numbered in order of their temporal occurrence. Arrows next to the relevant life stage show whether the impacts of warming temperatures are negative (points downwards) or positive (points upwards). *Note: Blaufelchen and Gangfisch colouration is, respectively, not really (in nature) bright blue and green.* (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

than in pelagic waters (Figary et al., 2023). Therefore, the spatial separation between where coregonine embryos incubate and where larvae develop could further contribute to asynchronies between larvae and prey developing. Understanding how past and future zooplankton phenologies have changed and could change at spatial scales relevant to the early life stages of ULC coregonines may help clarify whether phenological asynchronies between larvae and their prey already occur or may occur in the future.

Studies often focus on the impacts of climate on a consumer's (in this case, coregonines) interactions with prey, and how temperature changes might modulate these interactions with lower trophic levels. However, predation is an important driver of recruitment success that can also be modulated by changing temperatures: especially during the larval stage. Three-spined stickleback (*Gasterosteus aculeatus*) may be significant predators of embryonic and larval coregonines in Lake Constance (Gugele et al., 2020, 2023; Lucas et al., 2021; Roch et al., 2018; Rösch et al., 2018). It may be possible that warming temperatures increase stickleback predation on larval coregonines via a temperature-mediated increase in stickleback attack and consumption rates (Lefébure et al., 2014; Rahman et al., 2023). Additionally, adult stickleback will tend to be larger as water temperatures increase (Hovel et al., 2016), this suggests that a higher proportion of sticklebacks will be capable of consuming (due to a larger gape-size) larval fish below a certain size (Nilsson et al., 2019). Our study has also shown that climate change can potentially differentially alter phenology and growth patterns of closely related sympatric coregonines in Lake Constance. Hence, it is likely that future warming will lead to more complex, and possibly dissimilar, species–specific interactions between the lake's endemic coregonines and their predators.

Understanding the relevance of abiotic factors (e.g. temperature) on the early life of ULC *Coregonus* spp. is urgent due to the recent collapse of the coregonine fishery in the lake. In 2022, professional fishermen caught less than 10 % of the expected coregonine yield. As a result of this sudden decline, beginning in 2024, a three-year ban on all fishing equipment which targets coregonines has been implemented in Upper Lake Constance. Additional efforts to support the stocks may be necessary. For example, a plan has been made to produce larvae in hatcheries, raising them to sizes (≥ 4 cm) which reduce the likelihood of larvae being predated upon by invasive sticklebacks (Roch et al., 2018). Other techniques, including assisted gene flow (Aitken and Whitlock, 2013; Pregler et al., 2023) and stocking fish when plankton densities are adequate (Anton–Pardo and Adámek, 2015) could be used, though potential negative impacts of stocking on natural selection should not be ignored (Anneville et al., 2015; Eckmann, 2012; Thomas et al., 2009; Baer et al., 2023). We summarise current and future issues facing Lake Constance coregonine stocks and potential solutions in Appendix Table 4 of the supplementary materials. The results of our study can help inform fishery biologists and fishery stakeholders on how they can manipulate temperature to minimise embryonic mortality, control hatching dates, and maximise larval growth and performance. Particular results of this study, such as the contrasting impacts of incubation temperature on Blauflechen and Gangfisch larval traits, can be used to help design incubation and rearing protocols that are species–specific and focused towards achieving specific goals.

Aside from the negative impacts on Lake Constance's fishery, the decline of the coregonine populations in the lake has significant ecological ramifications. The coregonines of Lake Constance act as keystone species within the ecosystem (Baer et al., 2022b; DeWeber et al., 2022); coregonines, as planktivores, couple lower (zooplankton) and higher (piscivorous fish) trophic levels (Ljungström et al., 2020). Therefore, a decline in coregonine biomass could have rippling effects on zooplankton community dynamics (Zhang et al., 2019) and piscivorous fish populations (Diana, 1987; Soudijn et al., 2021). Reductions of larger fish species biomass can result in smaller, lower trophic level species occupying vacant niche space left by the absence of larger species. Such shifts decrease an ecosystem's overall trophic level and complexity and could also increase ecosystem instability (Chen et al., 2011; Uusi-Heikkilä et al., 2022). Fish populations can contribute to the nutrient demands of primary producers (Sharitt et al., 2021). Hence, a reduction in fish biomass could lead to reduced productivity within an ecosystem. Additional investigations of trophic interactions within the Lake Constance food web (Ogorelec et al., 2021), and how their disruption affects ecosystem functioning (Thomson et al., 2012), will help researchers understand what the secondary effects of coregonine stock declines could be.

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CRediT authorship contribution statement

Barnaby John Roberts: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing, Resources. **Christoph Chucholl:** Data curation, Formal analysis, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Alexander Brinker:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2024.102351.

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