Multiple climate change stressors reduce the emergence success of gravel-spawning fish species and alter temporal emergence patterns

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HIGHLIGHTS

- Multiple stressor interactions on fish emergence were tested in flume experiment.
- Mortality increased over time, accumulating to 91–100 % in key freshwater fish species.
- Across stressor treatments, average hatching rate was 37 % and emergence rate 18 %.
- Fine sediment led to highest mortality, exacerbated by warming and low-flow.
- Preventing extinction of gravel-spawning fishes requires mitigation and restoration.

GRAPHICAL ABSTRACT
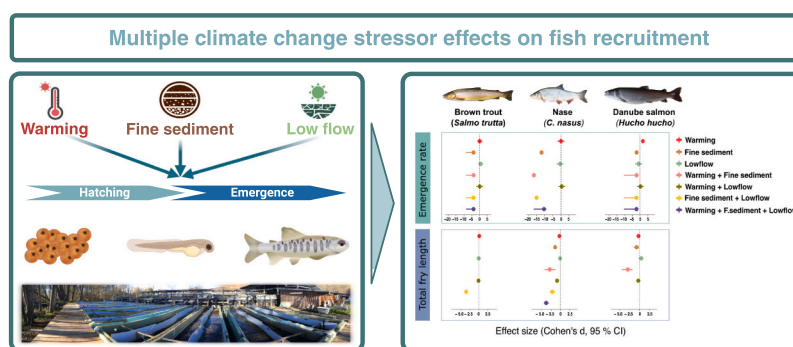
ARTICLE INFO

ABSTRACT

Climate change, with its profound effects on stream sediment, hydrological, and temperature dynamics, will exacerbate impacts on habitat conditions for many species, particularly those with vulnerable early life stages relying on the hyporheic zone, such as gravel-spawning fishes. Due to the complex and interactive nature of multiple stressor effects, we employed large-scale outdoor mesocosms to systemically test how the reproductive success of three gravel-spawning fish species brown trout (*Salmo trutta*), nase, (*Chrondrostoma nasus*) and Danube salmon (*Hucho hucho*) was affected by individual and combined effects of warming (+3–4 °C), fine sediment (increase in <0.85 mm by 22 %) and low-flow (eightfold discharge-reduction). Fine sediment had the most detrimental effect on emergence rate and fry length in all three species, reducing the emergence rate to zero in brown trout, 9 % in nase, and 4 % in Danube salmon. The emergence mortality caused by fine sediment surpassed that of hatching distinctly, suggesting that negative effects due to hypoxia were considerably exacerbated by entombment. Warming had only minor effects as a single stressor, but low flow reduced emergence rates of the spring spawning species nase and Danube salmon by 8 and 50 %, respectively. In combined treatments including fine sediment, however, the emergence success of all three species responded strongly negatively, even in the cyprinid species nase, which showed little interactive effects between stressors regarding hatching success. Warming and fine sediment also led to the earlier emergence of fry, implying a risk of asynchrony with available food resources. This study dramatically shows that climate change can have deleterious impacts on the reproductive success of gravel-spawning fish species, irrespective of taxonomic or ecological traits.

1. Introduction

Freshwater fish are severely threatened by numerous human-induced pressures like habitat degradation, pollution, and alterations in water flow, that affect ecosystems and organisms in complex ways (Dudgeon et al., 2006; Geist, 2011). In central Europe, changes in riverine fish communities have largely been driven by changes in land use, river impoundments and urban development (Bierschenk et al., 2019; Mueller et al., 2020), with most of these processes being largely irreversible (Auerswald et al., 2019). Climate change exacerbates the situation for many freshwater species as predicted temperature increases and changes in precipitation patterns will interact with present stressors in complex and variable ways (Dudgeon, 2019). Depending on the stressor, multiple-stressor interactions are complicated to predict and have been shown to rely on a series of factors such as life history traits, spatial and temporal scales as well as ecosystem type (Birk et al., 2020; Morris et al., 2022; Mueller et al., 2020; Wild et al., 2023). Meta-analyses of multiple stressor effects on freshwater organisms revealed that more than half of stressor responses in aquatic environments were larger (synergistic) or smaller (antagonistic) than the additive combination of single stressors would have suggested (Birk et al., 2020; Jackson et al., 2016; Schinegger et al., 2016), offering a high likelihood for ecological surprise effects in freshwater ecosystems.

While climate change affects freshwater ecosystems in a complex mixture of abiotic and biotic stressors, the most prominent implication is the rise in projected average global atmospheric temperatures, ranging from 2 to 3.5 °C and potentially reaching 5 °C by the end of the century (IPCC, 2021), which will consequently elevate water temperatures depending on hydrological, meteorological and land use characteristics of streams (Drainas et al., 2023). Temperature plays a crucial role in regulating metabolic and physiological processes in ectothermic freshwater organisms (Boltana et al., 2017; Magnuson et al., 1979), and complex spatiotemporal temperature patterns govern biological distribution patterns (Pander et al., 2024). Consequently, the effects of warming on these organisms have the potential to significantly impact freshwater ecosystems, ranging from changes in physicochemical properties to effects on individual organisms, entire communities, biological interactions and phenology (Khaliq et al., 2024; Krabbenhoft et al., 2014; Woodward et al., 2010). Depending on latitude and season, implications of changes in precipitation patterns and the hydrological cycle are more extended drought periods and more frequent and intense flood events (Forzieri et al., 2014; Kaule and Frei, 2022; Palmer and Raisanen, 2002). This is particularly relevant in the winter months when a transition from snow- to rain-dominated precipitation can change discharge dynamics (Rojas et al., 2012) and critical stream bed properties, including fine sediment deposition (Hoess and Geist, 2020). Increased precipitation and heavy rainfall events are associated with higher quantities of fine sediment entering streams and rivers (Mano et al., 2009). This can be attributed to erosion caused by discharge and alterations in soil characteristics (Bayard et al., 2005) and vegetation coverage in riparian zones (Herringshaw et al., 2011), ultimately resulting in a higher runoff volume.

The alterations in temperature, sediment composition, and hydrology in streams have been demonstrated to significantly impact the reproductive success and development of fish offspring, particularly in the vulnerable early life stages of lithophilic fish species (Duerregger et al., 2018; Jonsson, 2023; Rosenfeld et al., 2024; Wild et al., 2023). The high susceptibility of lithophilic fish to environmental perturbations results from their complex life cycle and their dependence on functional stream substrates as they utilize gravel bars to dig redds (brown trout and Danube salmon) (Smialek et al., 2021) or deposit their eggs on top of the substratum from where eggs drift into the interstitial pore space (nase) (Duerregger et al., 2018). The eggs then incubate in variable, species-specific depths until hatching (Grost et al., 1991; Nagel et al., 2020). During this time, larvae (until hatching) and alevins (past-hatching) remain in the safety of the substratum interstices until yolk

sacs have been fully absorbed and eventually emerge to the surface as fry. Various studies have demonstrated that fine sediment, typically defined as particles smaller than 2 mm, has a distinctively adverse impact on egg survival and larval development (Nagel et al., 2019; Sternecker and Geist, 2010; Sternecker et al., 2013). This is primarily due to fine sediment particles physically obstructing interstitial pore spaces, thereby impeding the exchange of water between the hyporheic zone and surface water, restricting oxygen availability for the development of fish embryos, and eliminating egg metabolic waste products (Greig et al., 2005; Jensen et al., 2009; Rubin and Glimsäter, 2005). However, fine sediment does not only inhibit the larval development of lithophilic fish larvae, but the clogging of stream bed interstices can also create a physical barrier that impedes the capability of hatched larvae to emerge to the surface, potentially trapping them in the substratum, also referred to as entombment (Sear et al., 2008; Sternecker and Geist, 2010). The probability of successful larval emergence increases with the coarseness of the substrate and the decrease in fine sediment content, highlighting the vast importance of functional incubation substrate for the entire developmental process from egg to emergence (Franssen et al., 2012; Nagel et al., 2019; Witzel and MacCrimmon, 1983). The hyporheic environment may experience a further decrease in oxygen concentrations due to warming, predominantly caused by the reduced solubility of oxygen in warmer water and the heightened oxygen consumption linked to increased metabolism (Piatka et al., 2021). Temperature has great potential to affect the development of salmonid embryos as their survival is highest at species-specific thermal optima (Ojanguren and Braña, 2003), and various life history traits later on in life, such as metabolism and growth are also temperature-dependent (Durtsche et al., 2021; Jonsson and Jonsson, 2019). Also, low flow and drought can reduce the oxygen availability and hence survival rates of developing fish embryos as oxygen is delivered at lower flow rates (Curry and MacNeill, 2004), and less turbulence can result in reduced oxygen inputs into the water body. While the effects of the described climate change stressors on early larval development of lithophilic fish species are well described for single stressors, particularly concerning fine sediment (Duerregger et al., 2018; Sear et al., 2016) and warming (Hari et al., 2005; Jonsson, 2023; Kamler et al., 2005), distinctly less information is available for two-way interactions of named stressors (Mari et al., 2021; Martin et al., 2017; Santiago et al., 2020). To date, only one study has simultaneously considered the effect of fine sediment, warming and low flow on the hatching success of the three lithophilic species brown trout (*Salmo trutta* L.), Danube salmon (*Hucho hucho* L.) and European nase (*Chondrostoma nasus* L.) (Wild et al., 2023). These three fish species differ regarding several life-history traits, eco-physiological requirements, and geographical distribution patterns across Europe. Brown trout (*Salmo trutta* L.), the most abundant representative of the salmonid family in Europe, has a large native range across Europe, North Africa, and Western Asia (MacCrimmon and Marshall, 1968) but has been introduced globally due to its adaptability and recreational fishing value (Klemetsen et al., 2003). However, the brown trout, once widely distributed, has now been classified as "endangered" on the Red List for freshwater fish and lampreys in Germany (Freyhof et al., 2015). As is typical for salmonids, brown trout are stenothermic cold-water adapted fish that dwell in well-oxygenated streams and rivers. Spawning typically occurs during autumn and early phases of winter, albeit the precise timing varies based on geographical latitude and specific environmental factors (Jonsson and Jonsson, 2011). Water temperatures during embryonic development optimally range between 7 and 10 °C (Ojanguren and Braña, 2003; Smialek et al., 2021). The duration of egg incubation to hatching strongly depends on water temperature, with average sums of degree days ranging between 532 and 554 (Jungwirth and Winkler, 1984; Sternecker et al., 2014). The second representative of the salmonid family, the Danube salmon (*Hucho hucho*), is the largest salmonid in European streams and is endemic to the Danube catchment. Its distribution covers tributaries and main channels of the Danube River in countries such as Germany,

Austria, Slovakia, Hungary, Romania, and Serbia (Holcik et al., 1988). It is currently listed as "endangered" on the IUCN Red List due to habitat degradation, pollution, overfishing, and dams hindering their natural migration and reproduction (Freyhof et al., 2015). Danube salmon are also cold-stenothermic fish, which limits their distribution range with respect to future global warming predictions (Pinter et al., 2024). Danube salmon spawn from March to May (Holcik et al., 1988) in water temperatures of 6–12 °C (Jungwirth and Winkler, 1984) with an average development time of 277–280 degree days (Sternecker et al., 2014). The cyprinid species European nase (*Chrondrostoma nasus)* was once abundant across most river systems of Europe and has similarly suffered strong population declines, being now considered a target species for conservation in Central European rivers (Schiemer et al., 2002). Nase start spawning between March and May, when a minimum water temperature of 8 °C is reached (Winkler et al., 1997) with eggs developing optimally if water temperatures during incubation range between 8 and 12 °C (Ahnelt and Keckeis, 1994; Schiemer et al., 2002). Under these conditions, nase larvae require 130–160 degree days until hatching (Penaz, 1974). Nase is adapted to warmer water temperatures, with highest fry survival at water temperatures up to 25 °C (Keckeis et al., 2005b). Assessing how individual eco-physiological requirements and life-history traits modulate the species' susceptibilities to climate change stressors in the egg-to-hatching phase has been the first important step (Wild et al., 2023). However, analyzing and understanding where and when individual and combined stressor effects are most influential along the entire egg-to-fry process also requires accurate estimates of how the final step of larval development, the post-hatching and emergence phase, is affected. To study the emergence process in the three described fish species, we used a mesocosm approach with 24 stream flumes. This setup enabled us to study the individual and combined effects of warming, fine sediment, and low flow on the emergence success of the two cold-water salmonid species brown trout and Danube salmon and the warm-water adapted cyprinid nase in a 3-way replicated fully crossed design addressing the following research questions:

1. What are the magnitudes of the individual effects of warming, fine sediment, and low flow on the emergence success and temporal emergence pattern of the three lithophilic fish species, brown trout, nase, and Danube salmon? How do they compare, and do combined effects act in an additive, synergistic, antagonistic, or reversed manner?
2. How do species-specific life history traits such as temperature preference, spawning seasonality, and larval size at emergence influence the species' susceptibility to climate change stressors?
3. Which component of the developmental processes (pre-hatching vs. post-hatching) is most strongly affected by the three climate change stressors and their interactions, and how does this relate to the overall potential of the species to respond to future climate change scenarios?

2. Material and methods

2.1. Set-up of the experimental flume mesocosms

For studying the individual and combined effects of the three climate change stressors, warming, fine sediment, and low flow in a 3-way fully crossed, replicated design (8 treatments, replicated 3 times each), we used a large-scale mesocosm set-up consisting of 24, 7 m long individual flumes as described in Wild et al. (2023) (Fig. 1).

The temporal and spatial set-up of bioindication experiments, including the partially simultaneous assessment of hatching rates using egg sandwich boxes (Wild et al., 2023) is illustrated in Fig. 2.

In short, we installed a customized air-source heat pump (Thorsten Meis Kälte Klima Lüftungstechnik, Siegburg, Germany) to mimic climate change conditions concurring with the RCP 8.5 scenario (IPCC, 2021) and increased water temperatures by 3.5–4 °C in the warming treatment

(Table S1). The reference sediment treatment was attributed an average proportion of fine sediment (<0.85 mm) of 6 ± 0.3 %, while in the fine sediment treatment, the proportion of fine sediment was increased to 28 ± 2.9 % based on field sediment analyses and literature values as described in Wild et al. (2023). The flow rate in the reference flow treatment, representing normal discharge conditions, averaged 4.8 ± 0.3 L/s, while a low flow rate of 0.6 ± 0.04 L/s was established to imitate drought conditions in the low flow treatment (Table S2).

2.2. Physicochemical measurements

We used water temperature loggers from *Onset* Computer Corporation (Bourne, MA, USA) to monitor surface and interstitial water temperatures in 10 cm substratum depth (see Wild et al., 2023 for more details). Hyporheic temperature data was used to calculate degree days (DD) as a measure of development time from fertilization to the day of emergence and was calculated by summing the daily mean temperatures over the developmental period for each emerged fry.

We measured oxygen concentration (mg/L and saturation (%), pH, specific conductivity at 20 °C (µs/cm), and redox potential (mV) weekly in the surface water and the same parameters as well as ion concentrations (F^-, Cl^-, NO_3^-, NO_2^-, SO_4^{2-}, PO_4^{3-}) bi-weekly in the interstitial zone at 10 cm depth as described in Wild et al. (2023).

2.3. Emergence rates and length measurements

In a bioindication experiment, we determined emergence rates and total length of emerged fry of brown trout, nase, and Danube salmon using emergence traps that consisted of 30 cm high PVC tube with a diameter of 15 cm (Fig. S2). Cut-outs on the bottom and side parts were covered with 250 µm gauze to facilitate adequate water flow. Each of the emergence traps was buried to a depth of approx. 15 cm. The bottom of the trap was covered with 5 cm of sediment, and 200 of the respective eggs were then evenly distributed and carefully covered with sediment so that eggs were buried to a total depth of 8–10 cm. In total, 4800 eggs were buried in 24 emergence traps for each experiment of the three fish species. Brown trout eggs were buried on 26 November 2020, nase eggs on 2 April 2021 and Danube salmon eggs followed on 5 May 2021 due to the very cold spring in the year 2021, when Danube salmon spawning maturity was not reached before the start of May. Assessment periods for hatching (Wild et al., 2023) and emergence success overlapped for the species nase and Danube salmon. Fig. 2 provides a more detailed representation of the spatial and temporal set-up of emergence traps and egg-sandwich boxes in individual flumes of the mesocosm experiment.

We obtained brown trout eggs from 10 male and 10 female fish from the fish hatchery Nadler (Eching, Germany). Nase eggs were stripped from 4 female and 5 male wild fish caught by a local fishing association in the River Isen close to Dorfen from a genetically well-characterized stock (Stoeckle et al., 2022). Danube salmon eggs were obtained from 6 female and 4 male fish from the state aquaculture facility of Lower Bavaria, "Lindbergmühle" (Germany), which is also a genetically characterized stock (Geist et al., 2009). All fish eggs were carefully transferred to the emergence traps on the day they were stripped and fertilized. Around the expected onset of emergence, traps were checked daily for emerged fry. Using pipettes, these were removed, collected in a vial, and euthanized using a twentyfold overdose of MS 222 (Tricaine Methane Sulphonate) following Adam et al. (2013). Subsequently, fry were preserved in 70 % ethanol for later measurement.

To determine the total length of preserved fry, we used the modular imaging software cellSens (Olympus Corporation, Tokyo, Japan). Emerged brown trout and nase fry were photographed with a microscope (SZX10 stereo microscope, Olympus Corporation, Tokyo, Japan) with a DF PALPO $1\times$ objective (Olympus Corporation, Tokyo, Japan) and $0.8\times$ zoom setting and subsequently measured with the tool "polyline" in µm. As Danube salmon fry were partially too large for the
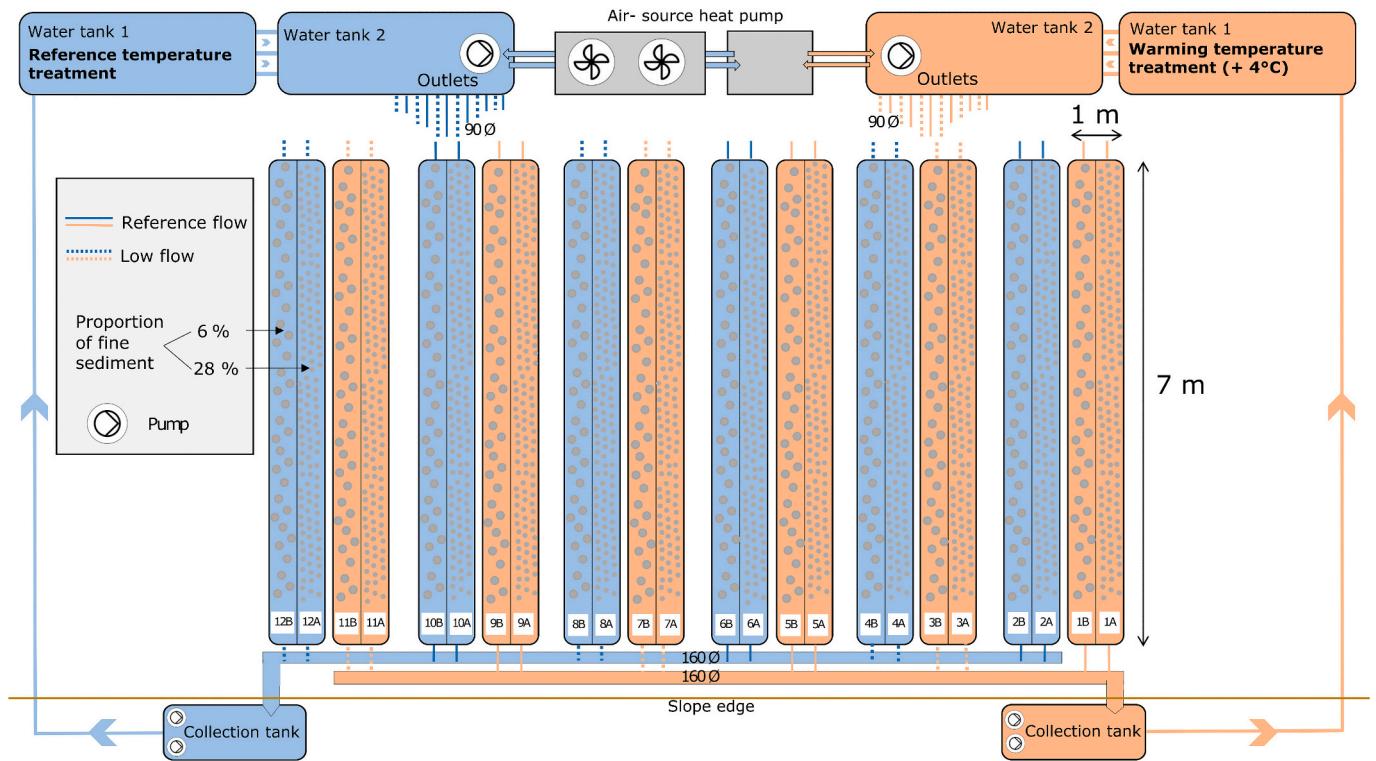
Fig. 1. Schmematic representation of the experimental flume set-up. Orange color represents flumes and technical installations associated with the water cycle of the warming temperature treatment, blue indicates flumes and installations of the reference temperature treatment. Small dots represent flumes with fine sediment treatment, larger dots indicate the reference sediment treatment. Flumes with reference flow conditions are denoted by straight lines at the top end of individual flumes, dotted lines indicate flumes running in the low flow treatment.
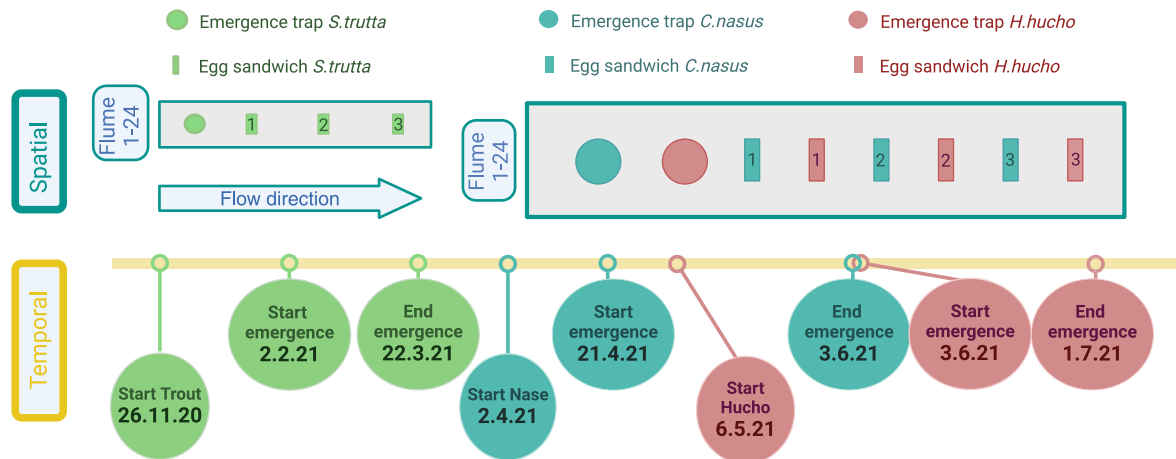
Fig. 2. Temporal and spatial set-up of bioindication experiments using egg-sandwich boxes to determine hatching success (Wild et al., 2023) and emergence success (this study) for the three fish species brown trout (*Salmo trutta*), nase (*Chondrostoma nasus*) and Danube salmon (*Hucho hucho*). Timing of egg burial in emergence traps and egg sandwich boxes is marked as "Start". Individual start and end dates of emergence are displayed for every species along the timeline. Dates are reported as day.month.year.

microscope, these were imaged using the CanoScan LiDE 400 scanner with a resolution of 600 dpi and measured using the "ImageJ" analysis program (Schindelin et al., 2012) with the tool "freehand selection."

2.4. Data analysis

All statistical analyses were conducted using R Studio Version 2023.12.1 + 402 (R Core Team, 2023). We tested for the individual and combined climate change stressor effects on emergence rates using linear models using the function "lm" with a "logit" transformation of the response variable. The models contained the fixed factors warming, fine sediment, low flow, and their interaction terms. We evaluated model fit based on diagnostic visualizations and parameters in DHARMa (Hartig, 2022) and using Akaike's Information Criterion (AIC) (Sakamoto et al., 1986).

We used linear mixed effect models (lmer) from the package "lme4" (Bates et al., 2015) with subsequent "Type II Wald chisquare tests" in the "Anova" function of the package "car" to analyze larval length at emergence as response vs. the three predictor variables warming, fine sediment, low flow, and their interactions. However, as individual fish

fry served as replication units in this analysis, we added a random intercept term for the individual flume where the emergence traps were placed. As less than three fry emerged in treatments containing fine sediment in the brown trout and Danube salmon experiment, the predictor variable "fine sediment" was excluded from these two models, and length was only discussed on a descriptive level.

To assess which of the three stressors and their interactions significantly affected the total duration of larval development until emergence, we used a linear mixed effects model (lmer) to relate the response variable "days to emergence" to the three stressors and their interaction terms. To account for spatial dependence among fry from the same trap/flume we included a random intercept for flume in the model and checked model assumptions using the "Dharma" package.

We calculated effect sizes of individual and combined climate change stressors on emergence rates and larval length using the function "bootES" in the package "bootES" (Gerlanc and Kirby, 2021). We used "Cohens d" as "effect-type," and the bootstrap method to calculate confidence intervals was set to "bca". To determine interaction typology among two-way stressor combinations, we used the package "multiplestressR" (Burgess and Murrell, 2022). 3-Way stressor interactions could unfortunately not be evaluated using this routine. The presence of interactions was hence only stated as such if they were statistically significant as calculated using linear and linear mixed models. Types of interactions were categorized according to Cote et al. (2016). If significance was not confirmed by methods mentioned above but showed tendencies in respect of synergisms, antagonisms, or reversals, as determined according to Cote et al. (2016), these types of interactions were only referred to as "trends."

Statistical significance was accepted at a p-value of <0.05.

3. Results

3.1. Environmental conditions in the experimental flume mesocosms

The eight treatments' environmental conditions across individual flumes remained constant (Table S1) from November 2020 to July 2021. The reference temperature treatment's mean interstitial water temperature was 7.73 ± 1.53 °C in the brown trout experiment, while the warming treatment's mean interstitial water temperature was 10.39 ± 1.86 °C (Table S2). The mean interstitial temperature in the nase experiment was 9.36 ± 1.23 °C in the reference and 12.45 ± 0.88 °C in the warming treatment. The average interstitial water temperature in the reference treatment of the Danube salmon experiment was 11.09 ± 1.94, while in the warming treatment, it was 13.93 ± 1.03 (Table S2). We determined the strongest differences in water chemistry between flumes with added fine sediment and those with reference sediment conditions (Table S1). In flumes with increased fine sediment content, the saturation of dissolved oxygen (DO) was reduced by half and showed higher variability ($52.3\% \pm 29.4$) compared to flumes with reference sediment conditions ($100.6\% \pm 8.0$).

3.2. Emergence rate

Across all treatments, a total of 1473 fry (31 %) emerged in the brown trout experiment, 1325 (28 %) in the nase experiment, and 153 (3 %) in the Danube salmon experiment. While emergence rates in reference treatments ranged between 77.8 % and 36.8 % in brown trout and between 55.6 % and 48.0 % in nase, in Danube salmon, only between 7.5 % and 1.9 % of the fry successfully emerged (Table 1).

Fine sediment had a consistent and significantly negative effect on the emergence rates of all three fish species (Table 1, Fig. 3, Fig. 5, Table S4). Fine sediment impeded the successful emergence of brown trout fry, resulting in a 0 % emergence rate (effect size (ES): brown trout: −4.0). Similarly, fine sediment reduced the emergence rate of Danube salmon and nase by 96 and 91 %, respectively (ES: Danube salmon: −2.2, nase: −12.9). Brown trout emergence rates were higher under low

flow conditions (+19.5 %), slightly lower in nase (−7.7 %), and distinctly lower in Danube salmon (−46.8 %). Warming, on the other hand, increased emergence success in the two salmonid species (+4.2 % in brown trout and +155.3 % in Danube salmon) and was neutral in nase (0 % change) (Table 1, Fig. 3, Fig. 5).

When combining the two stressors warming and low flow, the emergence rates of all three species increased (brown trout: +4.7 %, nase: +3.3 %, Danube salmon: +27.7 %).

The combined treatments of fine sediment and warming, however, reduced the emergence success by 100 % in brown trout, 90.7 % in nase, and 95.7 % in Danube salmon (Tables 1, 2). The emergence success of all fish species in the treatment combining fine sediment and low flow was similarly low (brown trout: −100 %, nase: −94.6 %, Danube salmon: −100 %).

When all three stressors were combined, emergence rates of both salmonid species were 0 % and severely reduced in the cyprinid species nase (−88.4 %) (Table 1, Fig. 3, Fig. 5).

3.3. Larval length at emergence

The mean total length of emerged fry in the two salmonid species was similar, amounting to 25.0 mm (range: 17.3–28.2 mm) in brown trout and 24.6 mm in Danube salmon (21.0–28.9 mm). The average length of emerged nase fry was 13.7 mm and ranged between 10.5 mm and 14.9 mm. The higher proportion of fine sediment led to a 3.0 % reduction of larval length at emergence in Danube salmon and 3.5 % decrease in nase (Table 3). As no brown trout fry had emerged from treatments containing a higher proportion of fine sediment, length measurements were unfortunately unavailable.

In Danube salmon, warming had a slight but negative effect, reducing larval length by 1.1 % (Table 3). Low flow, in contrast, increased larval length by 1.9 % (Table 3). In the spring-spawning species nase, the single stressors of warming and low flow significantly reduced larval length by 0.7 % and 0.2 %, respectively (Table 3, Table S5). In brown trout, the single stressors warming and low flow slightly increased brown trout larval length at emergence on average by 0.6 % and 0.1 %, respectively (Table 3, Fig. 4, Fig. 5).

However, if any of those single stressors were combined, consistently negative trends in total length were observed in all three assessed fish species. In treatments combining the stressors warming and fine sediment, we observed a synergistic trend: nase fry were, on average, 1.2 mm shorter (−7.7 %) and Danube salmon fry 3.1 mm shorter (−12.6 %) than fry from the reference treatment (Tables 3 and 4).

The stressor combination fine sediment and low flow equally produced smaller fish fry at emergence (brown trout: −13.6 %, nase −5.4 %).

Only nase fry successfully emerged from the three-way treatment combination of stressors, producing the strongest negative effect size calculated for length measurements (−11.2 %, ES: −3.53) (Fig. 4, Tables 3 and 4).

3.4. Temporal development

Brown trout eggs required a total mean development time of 90 days (68–116 days) and 755 DD (641–1172) until fry emerged from the substratum. Eggs of the two spring spawning species, nase and Danube salmon, developed distinctly quicker within a mean total development time of 37 days (19–62) in nase and 40 days (28–56) in Danube salmon. Nase required a mean of 387 DD (245–593), while Danube salmon needed, on average, 100 DD more with 487 DD (391–673).

The high variability in development time described above already indicates the pronounced differences in development time between eggs and alevins incubated within different treatments.

Overall, warming had the most significant effect on the duration of larval development until emergence in all three fish species (lmer: $p <$ 0.001, Table S6). In brown trout, fry emerged on average 22.6 ± 7.1

Table 1

Emergence rates (%) of the three fish species brown trout (*Salmo trutta* L.), nase (*Chondrostoma nasus* L.), and Danube salmon (*Hucho hucho* L.) within the seven stressor treatments and respective proportional changes in hatching rates in treatments versus reference conditions. Asterisks indicate significant effects (*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$) as tested by linear mixed effects models.

Treatment	Brown trout	%-change	Nase	%-change	Danube salmon	%-change
Reference conditions	57.3 ± 20.5		51.8 ± 3.8		4.7 ± 2.8	
Warming	59.7 ± 8.1	4.2	51.8 ± 15.1	0	12.0 ± 4.4	155.3
Fine sediment	0 ± 0	−100**	4.8 ± 3.5	−90.7**	0.2 ± 0.3	−95.7***
Low flow	68.5 ± 1.8	19.5	47.8 ± 9	−7.7	2.5 ± 2.3	−46.8
Warming + Fine sediment	0 ± 0	−100	2.2 ± 1	−95.8	0.2 ± 0.3	−95.7
Warming + Low flow	60.0 ± 9.8	4.7	53.5 ± 2.6	3.3	6 ± 4.4	27.7
Fine sediment + Low flow	0 ± 0	−100	2.8 ± 2.0	−94.6	0 ± 0	−100
Warming + Fine sediment + Low flow	0 ± 0	−100	6 ± 4.3	−88.4	0 ± 0	−100

days earlier and acquired 16 DD more in the warming treatment than in the reference treatment (Fig. 6). The warming effect was even more pronounced in the nase experiment, where fry emerged on average 28.5 ± 2.1 days earlier but with 170 DD less than in the reference treatment (Fig. 6). Danube salmon similarly emerged earlier (13.1 ± 3.5 days) and accumulated fewer degree days during that period (−32 DD).

Fine sediment significantly reduced the development duration of nase by 6.6 ± 3.3 days (lmer: $p < 0.001$, Table S6). Only very few fry emerged in the fine sediment treatment of the two salmonid species, hence, only the combined stressor effects of fine sediment and the other two stressors can be evaluated.

Low flow as a single stressor had a minimal but significant effect on the timing of emergence in nase −1 day (lmer: $p < 0.01$, Table S6). In brown trout, fry in low flow treatments emerged on average 0.7 ± 4.5 days later, and in Danube salmon, 4.0 ± 3.0 days later.

We determined a significant stressor interaction between fine sediment and warming in nase (lmer: $p < 0.001$) with nase emerging on average 31.0 ± 3.3 days earlier (−199 DD) in this treatment than in the reference (Table S6). In Danube salmon, only two fry emerged in the combined treatment of fine sediment and warming (18.9 days earlier, −114 DD), while no brown trout fry emerged in this treatment at all.

The combined effects of low flow and the two other stressors were additive: low flow with fine sediment led to brown trout fry emerging 10.3 ($n = 2$) days earlier and nase fry emerging 8.8 ± 1.8 days earlier. When low flow was combined with warming, brown trout fry emerged 22.1 ± 8.4 days (+15 DD) earlier, nase fry 30.1 ± 2.7 days (−196 DD) earlier, and Danube salmon fry 13.2 ± 4.9 days (−35 DD) earlier (Fig. 6).

In the combined treatment of warming, fine sediment, and low flow, nase fry emerged 32.9 ± 1.6 days and 230 DD before fry in the reference treatment.

Not only did the timing of emergence differ between the assessed stressors, but also the total length of fish fry along the emergence period, particularly at the onset of emergence (first two days), responded differently to stressors depending on the fish species. Along the timeline of the emergence period, nase and Danube salmon larvae grew continuously larger, while brown trout larvae exhibited some variability in total length at emergence, but the size range of emerged fry did not change distinctly over time (Fig. 7).

In nase, fry emerging in treatments containing fine sediment were smaller (−0.22 mm) than fry emerging concurrently from reference sediment treatments. This was particularly pronounced in treatments where fine sediment was combined with warming (−0.72) and in the treatment where all three stressors were combined (−0.83 mm) (Fig. 7).

Brown trout fry emerging from the warming treatment were 3.0 mm larger than fry in the reference temperature treatment when they emerged one month later (Fig. 7).

In the spring-spawning salmonid Danube salmon, this pattern was reversed. Danube salmon fry emerging in the warming treatment were, on average, 1.1 mm shorter than the fry emerging from the reference treatment approx. Two weeks later. Nase fry in the warming treatment were only slightly smaller (0.2 mm) than fry from the reference

treatment, which emerged approximately 29 days later and acquired 170 DDs more.

In the combined treatment of low flow and warming, brown trout fry were 1.9 mm larger than in the treatment combining low flow and reference temperature. Similarly, on average, Danube salmon fry in the low flow and warming treatments were 2.0 mm smaller than fry emerging in the low flow-reference temperature treatments 20 days later (Fig. 7).

4. Discussion

The findings of this experimental study are the first to offer an understanding of how multiple climate change stressors affect the entire egg-to-fry development of three lithophilic fish species, differing in multiple life-history traits such as thermal preferences or spawning seasonality. Variability in these traits led to vastly different responses of larval development until hatching (Wild et al., 2023), with fine sediment as a single stressor already leading to a significantly reduced hatching success (−80 % in brown trout, −52 % in nase, and −62 % in Danube salmon) (Wild et al., 2023). As emergence success is a composite measure of pre- and post-hatching processes, this study is the first to provide the opportunity to understand how the different developmental phases and the crucial final stage of fry emergence are impacted by the three climate change stressors and their interactions. Our data revealed that along the developmental path, fine sediment as a single stressor and interactive effects among stressors become even more detrimental to the reproductive success of gravel-spawning fish species.

4.1. Single stressor effects on emergence success and alevin development

The total egg-to-emergence survival, as determined in this study, was even more severely impacted than the previously studied hatching success, as no brown trout fry emerged from any of the individual or combined stressor treatments that included fine sediment (hatching success: 16 %). Similarly, in nase, only 4.8 % (hatching: 19 %) and in Danube salmon, only 0.2 % (hatching: 25 %) of fry emerged in fine sediment treatments, and even fewer in the combined treatments. This means that approx. 16 % (brown trout), 14 % (nase), and 25 % (Danube salmon) of additional mortality can be attributed to the emergence process. Much research has been conducted on the effects of fine sediment during the egg incubation period, particularly in salmonid species (Greig et al., 2005; Kemp et al., 2011; Sear et al., 2016; Sternecker et al., 2013) but also in lithophilic cyprinids (Bašić et al., 2018; Duerregger et al., 2018; Nagel et al., 2020). These negative implications of fine sediment are mainly attributed to the clogging of the interstitial pore space that inhibits the inflow of oxygenated water to the interstitial zone, thus leading to hypoxia and the accumulation of metabolic waste products that inhibit growth and hatching success, also referred to as asphyxiation (Greig et al., 2005; Milan et al., 2000; Sear et al., 2008; Wild et al., 2023). Concerning the constantly low oxygen concentrations measured in the interstitial zone of fine sediment treatments, it can be assumed that hatching rates and, thus, the developmental phase ahead
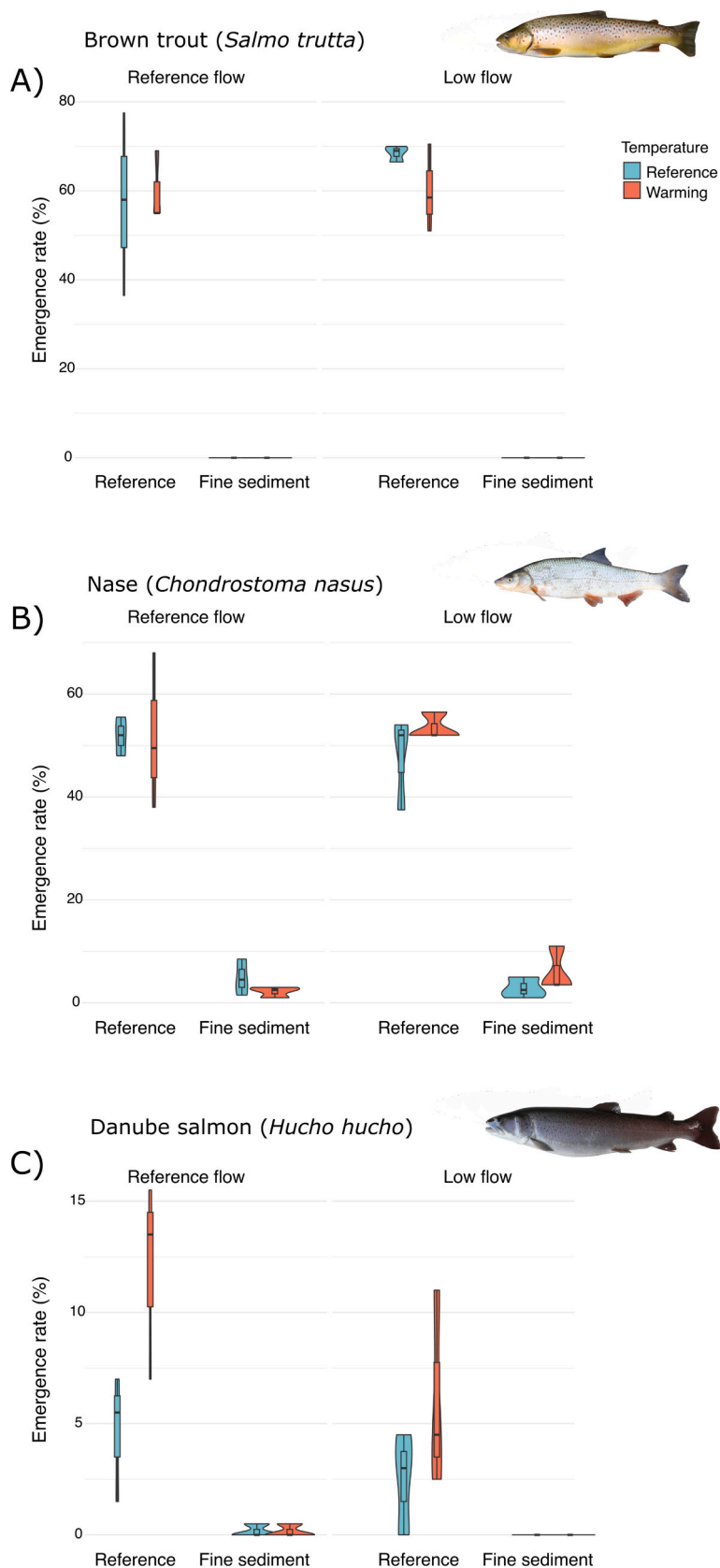
Fig. 3. Multiple stressor effects of warming, fine sediment and low flow on emergence rates of the three fish species brown trout (*Salmo trutta* L.), nase (*Chondrostoma nasus* L.) and Danube salmon (*Hucho hucho* L.). Violin plots represent kernel probability density of the data groups overlain with boxplots displaying the median and the 25 % and 75 % quantiles. Upper and lower whiskers extend to a maximum of 1.5 times the inter-quartile range.

Table 2

Interaction types determined by effect sizes of emergence rates of single stressors (in parentheses) and expected additive effects as well as the observed effect size in the three fish species brown trout (*Salmo trutta* L.), nase (*Chondrostoma nasus* L.), and Danube salmon (*Hucho hucho* L.).

	Emergence rate	Additive	Observed	Type of combined effect
Brown trout	Warming (0.15) + Fine sediment (−3.95)	−3.80	−3.95	Dominance
	Fine sediment (−3.95) + Low flow (0.77)	−3.19	−3.95	Dominance
	Warming (0.15) + Low flow (0.77)	0.92	0.17	Dominance
	Warming (0.15) + Fine (−3.95) + Low flow (0.77)	−3.04	−3.95	Dominance
Nase	Warming (0) + Fine sediment (−12.93)	−12.93	−18.04	Synergism (trend)
	Fine sediment (−12.93) + Low flow (−0.58)	−13.51	−16.26	Synergism (trend)
	Warming (0) + Low flow (−0.58)	−0.58	0.52	Antagonism (trend)
	Warming (0) + Fine (−12.93) + Low flow (−0.58)	−13.51	−11.31	Dominance/ antagonism (trend)
Danube salmon	Warming (1.97) + Fine sediment (−2.23)	−0.26	−2.23	Dominance
	Fine sediment (−2.23) + Low flow (−0.84)	−3.07	−2.32	Dominance
	Warming (1.97) + Low flow (−0.84)	1.13	0.36	Antagonism (trend)
	Warming (1.97) + Fine (−2.23) + Low flow (−0.84)	−1.10	−2.32	Dominance

of the emergence process were negatively influenced by these sedimentary properties. This suggests that larvae that hatched, already had developmental constraints such as reduced growth or bigger yolk sacs, which likely affected their ability to successfully move through the sediment matrix (Louhi et al., 2011; Roussel, 2007). This is also supported by the size of emerged fry incubated in fine sediment treatments, where nase fry were 3.5 % (0.5 ± 0.4 mm) smaller and Danube salmon fry 3 % (7 mm) smaller than fry in reference treatments, hinting at distinctly reduced developmental progress attributable to insufficient oxygen supply (Wild et al., 2023). As fry are dependent on an unobstructed interstitial macropore system that allows them to pass through to the surface, fine sediment has been shown to impede emergence success in a process called entombment as fry can become trapped due to a layer of colmated fine sediment sealing the substratum at the surface and/or fine sediment clogging the emergence paths of fry (Franssen et al., 2012; Nagel et al., 2019; Sear et al., 2008). A field study has shown that spring-spawning species are more susceptible to fine sediment deteriorating recruitment success than fall-spawning species, such as the brown trout, likely due to cooler water temperatures during winter (Sternecker et al., 2014). However, linking these findings on a

mechanistic level has been difficult in the field setting due to the black box character of interacting environmental factors influencing interstitial conditions. The standardized setting and comparable environmental conditions have been seen as crucial, yet missing aspect of field-based studies (Kemp et al., 2011).

Compared to other studies that assessed emergence rates in regard of fine sediment content, emergence rates of brown trout in this study were distinctly lower than in several other studies, such as an experimental study by Louhi et al. (2011), where emergence success under repeated additions of fine sediment was 55 %. In a study by Witzel and Mac-Crimmon (1983) brown trout emergence ranged between 96 and 77 % at sand proportions between 20 and 40 %, respectively. In a study on brook trout (*Salvelinus fontinalis*) by Franssen et al. (2012), a fine sediment proportion (<2 mm) of 22 % was associated with strongly reduced emergence success of <12 %. The high variability in the outcomes of these studies compared to ours likely derives from the study setting (experimental vs. field) and the different composition of incubation sediments and fine sediment proportions. Particularly, the relatively high content of 1.7 % of silt/clay (<0.063 mm) in the fine sediment treatments of our study might explain why the egg-to-fry success of salmonids was very low (Louhi et al., 2011). In the cyprinid species nase, the higher proportion of fine sediment in our study compared to the laboratory setup from Nagel et al. (2019) (28 % vs. 20 %) might also be responsible for why more nase larvae emerged in Nagel et al. (2019) compared to our study (55 % vs. 9 %). Particularly noteworthy concerning the emergence success of nase fry was the distinctly stronger effect of fine sediment on the emergence success compared to previously determined hatching rates (Wild et al., 2023). This indicates that nase larvae have the ability to endure suboptimal conditions during the embryonic phase better than salmonid larvae due to their lower demand for oxygen, but have a higher susceptibility for entombment during the emergence phase (Keckeis et al., 2005a, b). This is likely due to nase fry being smaller and having less robust physiology that hinders them from breaking through the sediment compared to salmonids. This emphasizes the profound influence that fine sediment can have on the reproductive success of nase, particularly on the emergence part of egg-to-fry survival.

Emergence rates of Danube salmon fry under reference conditions were comparably low (4.7 ± 2.8), given that the hatching success of Danube salmon in the reference treatment was, on average, 67 % (Wild et al., 2023). Danube salmon, particularly in the early life stages, are known to suffer high mortality rates when kept in aquaculture conditions (Geist et al., 2009; Holčík et al., 1988; Jungwirth, 1978). Correspondingly, Sternecker and Geist (2010) determined similarly low survival rates (4 %) despite higher hatching rates (100 %) of Danube salmon fry in their reference treatment, implying that developmental processes around the emergence might be a highly sensitive time period in the species' life history. To the best of our knowledge, no studies have yet analyzed fine sediment's effects on Danube salmon's emergence process. Sternecker and Geist (2010), however, looked at gravel size classes and showed that Danube salmon eggs that were incubated in fine gravel (5–8 mm) had a significantly lower emergence rate of 3 %

Table 3

Total larval length at emergence (mm) of the three fish species brown trout (*Salmo trutta* L.), nase (*Chondrostoma nasus* L.) and Danube salmon (*Hucho hucho* L.) within the seven stressor treatments and respective proportional changes of length in treatments versus reference conditions. Asterisks indicate significant effects (*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$) as tested by linear mixed effects models.
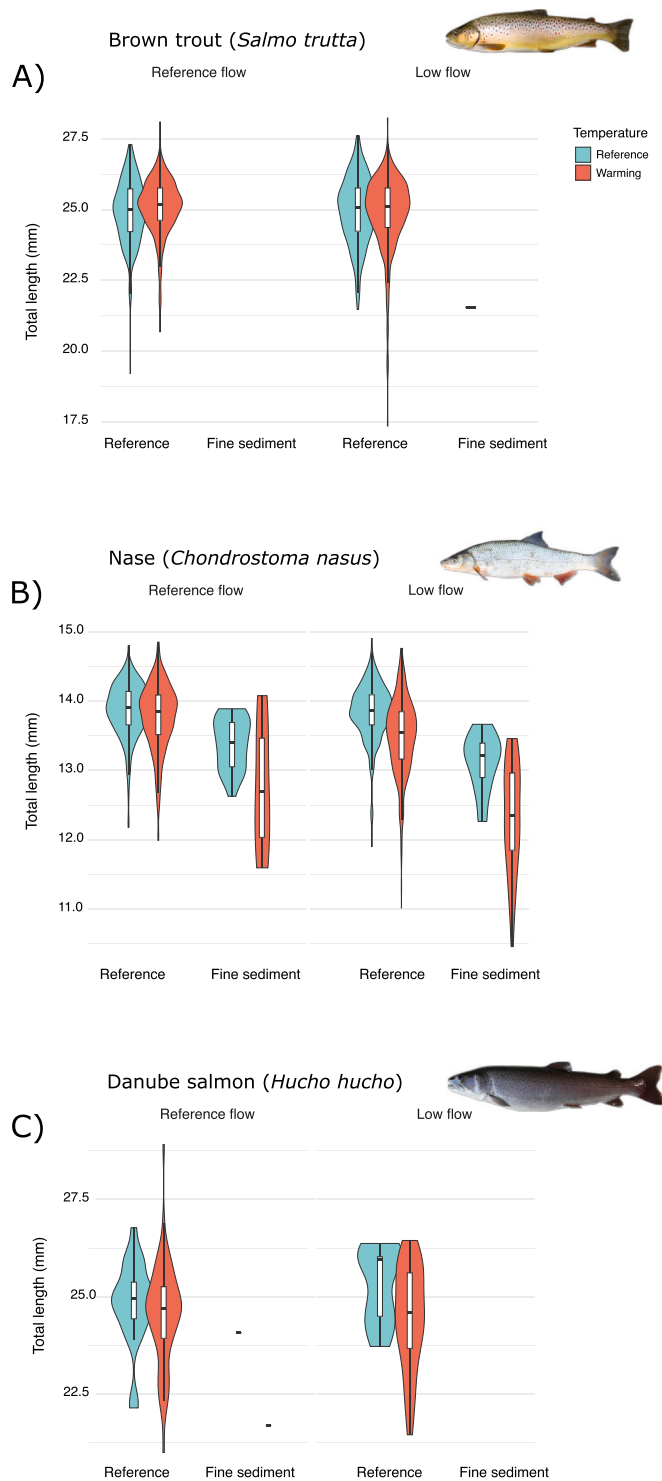
Treatment	Brown trout	%-change	Nase	%-change	Danube salmon	%-change
Reference conditions	24.9 ± 1.1		13.9 ± 0.4		24.8 ± 1.1	
Warming	25.1 ± 1.0	0.6	13.8 ± 0.5	−0.7**	24.5 ± 1.3	−1.1
Fine sediment			13.4 ± 0.4	−3.5***	24.1	−3.0
Low flow	25.0 ± 1.2	0.1	13.8 ± 0.40	−0.2*	25.3 ± 0.9	1.9
Warming + Fine sediment			12.8 ± 0.9	−7.7	21.7	−12.6
Warming + Low flow	24.9 ± 1.3	−0.3	13.5 ± 0.6	−2.8	24.5 ± 1.3	−1.4
Fine sediment +Low flow	21.5	−13.6	13.1 ± 0.4	−5.4		
Warming + Fine sediment + Low flow			12.3 ± 0.8	−11.2		

A) Brown trout (*Salmo trutta*)

B) Nase (*Chondrostoma nasus*)

C) Danube salmon (*Hucho hucho*)

Fig. 4. Multiple stressor effects of warming, fine sediment and low flow on total larval length at emergence depicted for the three studied fish species brown trout (*Salmo trutta* L.), nase (*Chondrostoma nasus* L.) and Danube salmon (*Hucho hucho* L.). Violin plots represent kernel probability density of the data groups overlain with boxplots displaying the median and the 25 %, and 75 % quantiles. Upper and lower whiskers extend to a maximum of 1.5 times the inter-quartile range.

compared to 91 % and 96 % emergence rates in coarser gravel (8–16 mm and 16–32 mm respectively) demonstrating that even grain sizes above the sand class can have detrimental effects on Danube salmon emergence success.

Warming as a single stressor had only minimal effects on emergence rates of brown trout and nase but led to increased length at emergence in brown trout (+3 mm) and a slight decrease in total length at emergence in nase (−1 mm). In Danube salmon, hatching rates initially showed a decrease of 8 % in the warming treatment (Wild et al., 2023). Emergence rates, however, increased from 4.7 % in the reference treatment to 12 % in the warming treatment (−3 mm in total length), suggesting an overall positive effect of warmer temperatures, likely due to quicker development and an associated shortened period of incubation risks (Keckeis et al., 2005b).

Low flow increased emergence success slightly in brown trout (+20 %) while nase and Danube salmon responded negatively (−8 % and −50 %, respectively). These results can be explained by divergent spawning habitat preferences of the fish species where brown trout is known to spawn in shallower and slower-flowing streams where flow velocities range between 20 and 55 cm/s (Louhi et al., 2008) while nase and Danube salmon prefer spawning habitats in larger rivers within the barbel fish region where flow velocities during spawning season typically range between 63 and 131 cm/s in nase (Melcher and Schmutz, 2010) and approx. 60 cm/s in Danube salmon (Ihuţ et al., 2014). As low flow slightly decreased hatching success in brown trout (Wild et al., 2023), it can be assumed that the effect of low flow depends on the developmental phase of respective fish species. As hatched fish larvae can move through the interstitial pore space to actively find more suitable conditions and possibly also avoid oxygen-deprived zones, their susceptibility to suffering from hypoxia and toxicological stress is lower. Also, the colder temperatures and higher oxygen concentrations during winter development might explain why a reduced water inflow might have had less pronounced consequences on brown trout regarding oxygen infiltration and water exchange between hyporheos and surface water. Given the consistently negative effects of low flow on the two-spring-spawning species, nase and Danube salmon, a reduction in discharge due to the loss of snow melt and the earlier onset of drought and periods of low flow in spring (Schneider et al., 2013) are likely to have negative effects on the egg-to-fry success of both species in temperate climate zones of Europe. Particularly in the Mediterranean distribution of the Danube salmon, reclining spring flows and drought during egg incubation have the greatest potential to deteriorate the reproductive success of Danube salmon (Magalhães et al., 2007; Papadaki et al., 2016).

4.2. Multiple stressor effects on emergence success and alevin development

In previously assessed hatching rates (Wild et al., 2023), synergistic interactions among multiple stressors occurred mainly in the two salmonid species. Regarding emergence success, multiple stressor effects in the two salmonid species were dominated by fine sediment, highlighting the overriding destructive effect of fine sediment on salmonid reproduction. While in the species nase, interactions among multiple stressors were scarce regarding hatching rates, stressor combinations affecting the egg-to-emergence process, as assessed in this study, showed a primarily synergistic trend, particularly between the stressor pairs fine sediment and warming and fine sediment and low flow. In terms of length of nase fry, combined responses were mostly negative and also showed a synergistic trend, even though when single stressor responses of low flow and warming were positive. This implies that warming and low flow might play a critical role in regulating emergence success, particularly in species with higher tolerances for fine sediment. The overall increase in mortality and developmental constraints compared to previously assessed hatching rates can be explained by the longer time period larvae and alevins remaining in the interstitial zone where incubation conditions can worsen with time (Greig et al., 2007; Louhi et al., 2011). Limited oxygen supply might be tolerable for species with intermediate oxygen demand, such as the cyprinid species nase, for a certain period. Over time, however, the combination of fine sediment
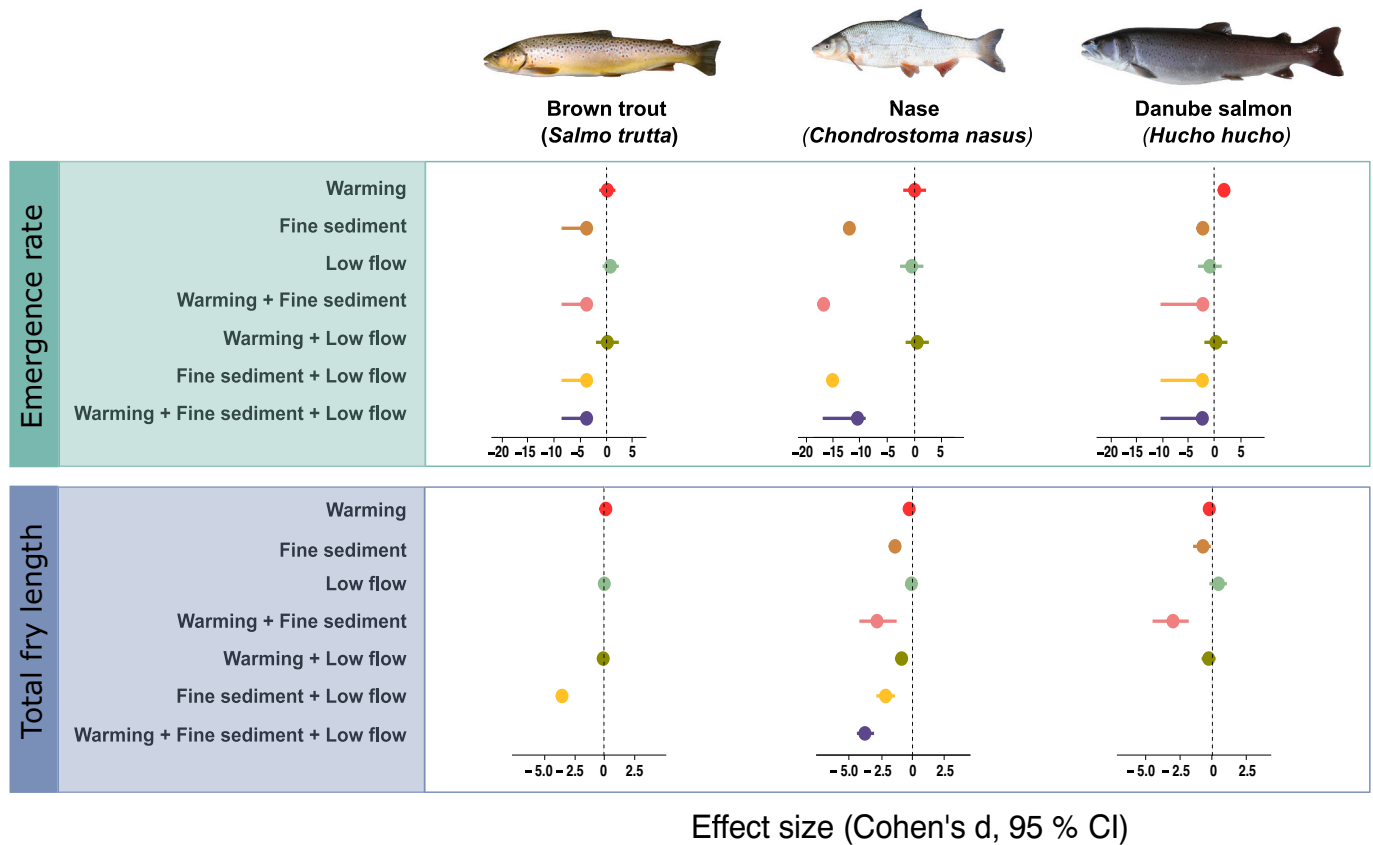
Fig. 5. Effect sizes of individual and combined climate change stressors warming, fine sediment, and low flow on emergence rates and total larval length at emergence in the three fish species brown trout (*Salmo trutta* L.), nase (*Chondrostoma nasus* L.), and Danube salmon (*Hucho hucho* L.).

Table 4
Interaction types determined by effect sizes of total larval length at emergence of single stressors (in parentheses) and expected additive effects as well as the observed effect size in the three fish species brown trout (*Salmo trutta* L.), nase (*Chondrostoma nasus* L.), and Danube salmon (*Hucho hucho* L.).

	Effect size of total length at emergence	Additive	Observed	Type of combined effect
Brown trout	Warming (0.14) + Fine (NA)	NA	NA	
	Fine (NA) + Low flow (0.03)	NA	−3.11	
	Warming (0.14) + Low flow (0.03)	0.16	−0.06	Reversal (trend)
	Warming (0.14) + Fine (NA) + Low flow (0.03)	NA	NA	
Nase	Warming (−0.24) + Fine (−1.29)	−1.54	−2.63	Synergism (trend)
	Fine (−1.29) + Low flow (−0.07)	−1.37	−1.99	Synergism (trend)
	Warming (−0.24) + Low flow (−0.07)	−0.32	−0.81	Synergism (trend)
	Warming (−0.24) + Fine (−1.29) + Low flow (−0.07)	−1.61	−3.53	Synergism (trend)
Danube salmon	Warming (−0.23) + Fine (−0.70)	−0.93	−2.92	Synergism (trend)
	Fine (−0.70) + Low flow (0.45)	−0.25	NA	
	Warming (−0.23) + Low flow (0.45)	0.22	−0.28	Dominance
	Warming (−0.23) + Fine (−0.70) + Low flow (0.45)	−0.48	NA	

and other stressors reduces oxygen concentrations and inflow beyond the tolerance levels of even more resistant species, while in less tolerant species, emergence success is already completely diminished by fine sediment as a single stressor. As with warming spring temperatures, oxygen concentrations will decline further in the interstitial zone, spawning time, and respective background temperatures will likely have an important effect on the magnitude of multiple stressor effects on species' reproductive success, particularly in alpine regions where salmonid species like brown trout and Danube salmon are adapted to year-round cold-water habitats (Hari et al., 2005; Scheurer et al., 2009).

4.3. Multiple stressor effects on temporal emergence patterns

Temporal emergence patterns were most strongly affected by warming in all three species, accelerating the onset of emergence on average by 23 days in brown trout, 29 days in nase, and 13 days in Danube salmon. However, while brown trout fry in the warming treatment were also larger (3 mm) at the onset of emergence compared to reference ones, Danube salmon fry were 1.1 mm shorter in the reference treatment, while nase fry had the same size. As ectothermic fish, larvae, and alevins develop faster in warmer water (Jonsson and Jonsson, 2009), the timing of alevin emergence can vary considerably depending on variations in water temperatures (Elliott and Elliott, 2010). Nonetheless, the magnitude of these temporal changes with approx. 1 month in brown trout and nase and 2 weeks in Danube salmon can have pronounced effects on the survival and fitness of emerged fish fry due to a temporal mismatch with food availability (Cushing, 1990). Also, warmer temperatures during embryonic development can affect ecological traits and influence the fish's ability to rapidly adapt to changing environments via epigenetic mechanisms (Jonsson and Jonsson, 2019). Brown trout fry in the warming treatment did not grow larger over the period of emergence, in contrast to nase and Danube
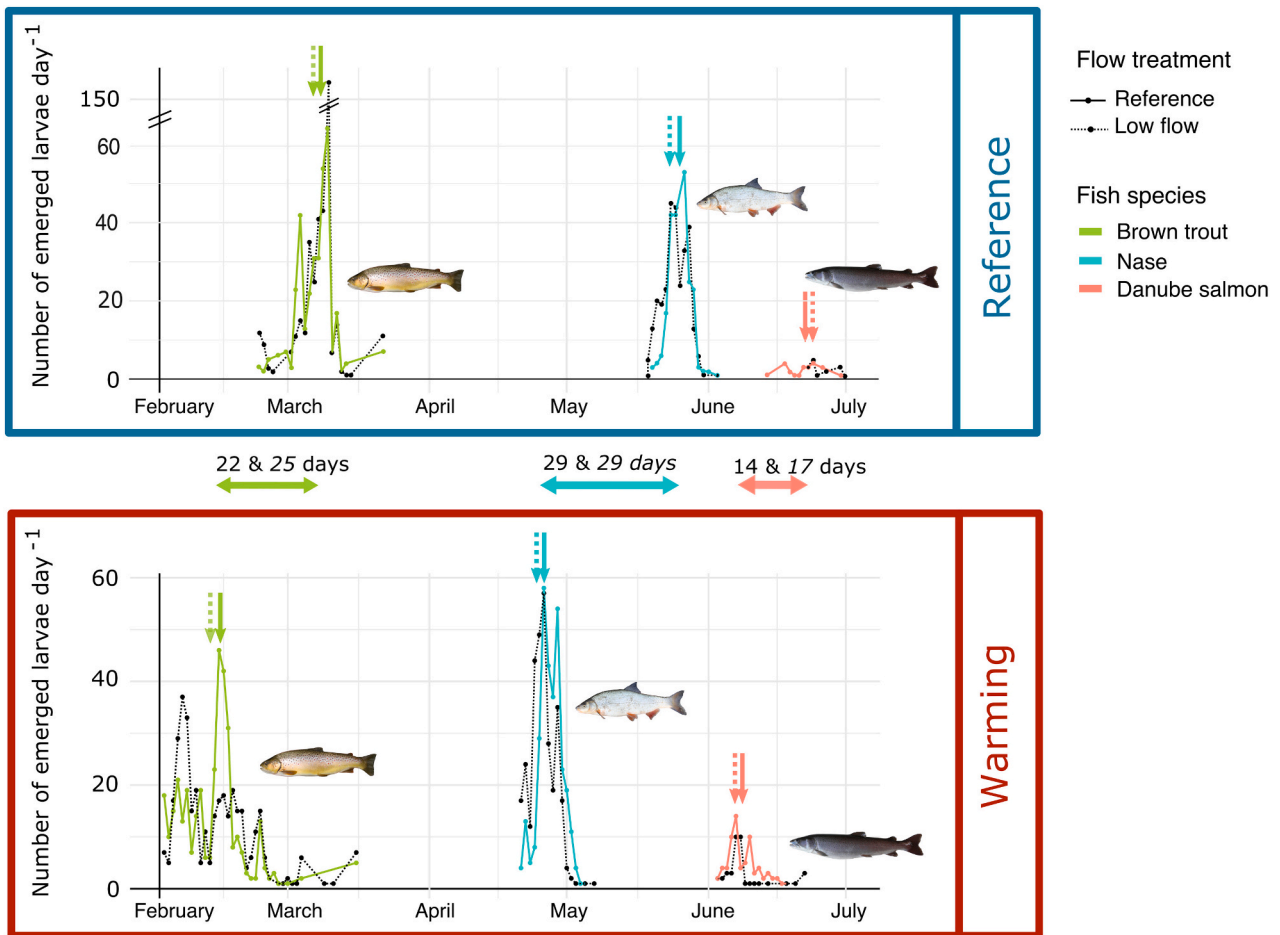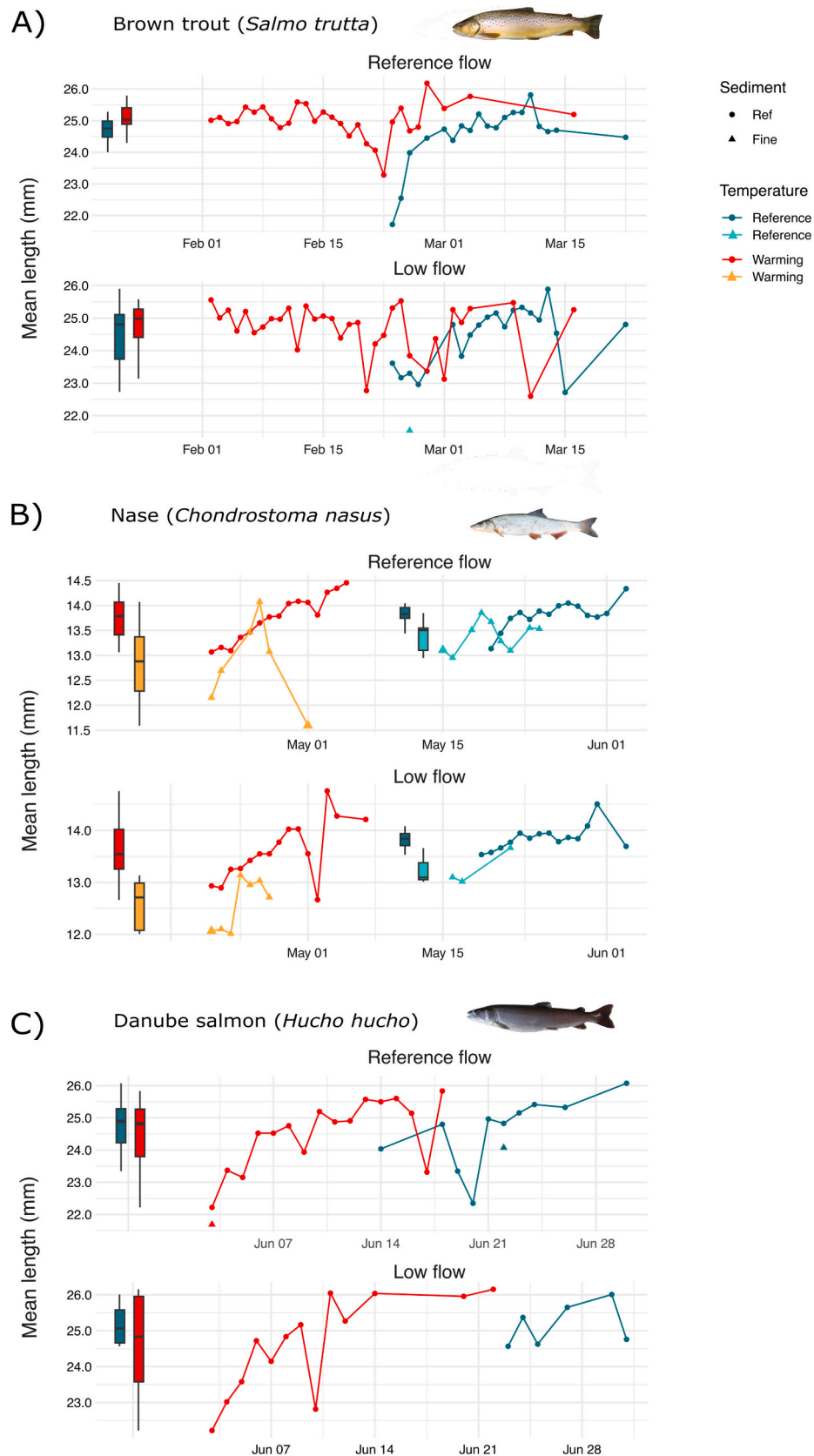
Fig. 6. Temporal emergence patterns in the three fish species brown trout (*Salmo trutta* L.), nase (*Chondrostoma nasus* L.), and Danube salmon (*Hucho hucho* L.) in the warming (red) and reference temperature treatments (blue). Solid lines indicate reference flow conditions and dotted lines show low flow conditions. Correspondingly, dotted downward-facing arrows indicate the duration until 50 % of fry have emerged in low flow treatments. Solid arrows denote the median emergence duration in the reference flow treatment. Horizontal arrows show the difference in the median duration of larval emergence in the respective fish species between warming and reference temperature treatments. Numbers in italics represent the difference in duration between low flow treatments, while standard font type indicates the difference in duration for reference flow conditions. As only very few fry emerged from fine sediment treatments, these points were excluded to improve the clarity of the figure. Note the y-axis is discontinuous in the reference temperature panel to accommodate the one-day event when brown trout fry emergence surpassed 150 individuals.

salmon fry whose total length at the end of the emergence phase was distinctly larger than at the beginning. The increasing length of emerging fish fry with time has also been documented in other studies, e. g., in nase (Nagel et al., 2019). For salmonids, very little information is available on this topic, but Réalis-Doyelle et al. (2018) have documented considerable impacts of higher temperatures (12 °C) on brown trout development, describing developmental delay and low energy reserves in fish alevins incubated at 12 °C compared to incubation at 4 and 6 °C. As a result, fish larvae might have used most of their energy allocation in the yolk sac for their metabolic expenditures at warmer temperatures and had little possibility to invest this energy into growth (Kamler, 2002).

Fine sediment as a single stressor accelerated the emergence of nase fry by 7 days and reduced their size at the onset of emergence by 0.22 mm, and, for combined treatments of fine sediment and warming and low flow, between 0.7 and 0.8 mm. This pattern of premature hatching and emergence as a response to high proportions of fine sediment has been observed by other authors (Bowerman et al., 2014; Franssen et al., 2012; Louhi et al., 2011; Nagel et al., 2019) and can be interpreted as an emergency behavior to avoid unfavorable environmental conditions in the sediment. Often, this behavior is associated with fry emerging with larger yolk sacs that subsequently limit their ability to navigate and

swim efficiently, thus making them more susceptible to predation (Louhi et al., 2011; Roussel, 2007).

The assessment of three multiple stressors and their interactions, as carried out in this systematic study, under controlled conditions, already demonstrated deleterious impacts on the reproductive success of fish species across various ecological and physiological requirements. Given that natural stream ecosystems often face many additional concurrently occurring and interacting stressors such as nutrients, contaminants, habitat alteration, and invasion (Bierschenk et al., 2019; Birk et al., 2020; Bruder et al., 2017), real-life effects are expectedly even more dramatic. This is already observed in the population trends and projections of population trends for many freshwater fish species, particularly those of gravel-spawning species (Heino et al., 2015; Olden et al., 2010; Ricciardi and Rasmussen, 2001). While the conservation status of the Danube salmon has been critical for a longer time due to its endemism in the Danube catchment (Freyhof et al., 2015; Ratschan, 2014), now even the previously ubiquitously distributed brown trout has recently been listed as "endangered" on the Red List for freshwater fish and lampreys in Germany (Freyhof et al., 2015) highlighting the drastic implications climate change will unceasingly have on cold-water adapted species.

Fig. 7. Temporal patterns of mean larval length during emergence for the three fish species brown trout (*Salmo trutta* L.), nase (*Chondrostoma nasus* L.) and Danube salmon (*Hucho hucho* L.). Temporal patterns are presented according to flow conditions (upper panel = reference flow and lower panel: low flow flow), temperature conditions (dark red and orange = warming temperature, blue and turquoise = reference temperature) and sediment composition (circle = reference sediment, triangle = fine sediment). According to this terminology, boxplots are provided to summarize mean larval lengths of temporal patterns for given treatment combinations.

5. Conclusion and outlook

This study provides new and systematic insights about the magnitude as well as the directionality of stressors and their interactions. It demonstrates vastly negative effects of the assessed climate change stressors, exemplifying that fine sediment severely reduces the emergence success of all three fish species due to the risks of asphyxiation and entombment and that these effects grow more deleterious the longer eggs, larvae, and alevins are exposed to these conditions in the incubation substrate. These effects are exacerbated by warmer background temperatures and lower flow rates during incubation. Climate change is unlikely to be brought to a halt in the foreseeable future (Dvorak et al., 2022), and with that, an increase in atmospheric temperatures and the frequency of hydrological alterations will have to be considered as new ecological baseline conditions. Therefore, it is paramount to tackle anthropogenic stressors that can be actively mitigated and restore riverine ecosystems in a holistic and catchment-based manner (Bernhardt and Palmer, 2011; Mika et al., 2010; Staponites et al., 2022). Within a central approach to buffer hydrological and temperature extremes and retain fine sediment and nutrients in urban and agricultural areas, priority should be given to the restoration of flood plains and the restoration of broad, complexly vegetated buffer zones along streams to mitigate the effects of multiple stress in the context of climate change while concurrently safeguarding domestic and food security (Auerswald et al., 2019; Feld et al., 2018).

CRediT authorship contribution statement

Romy Wild: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christoffer Nagel:** Writing – review & editing, Methodology, Investigation, Data curation. **Juergen Geist:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Conceptualization.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.175054.

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