Elevated temperature and deposited sediment jointly affect early life history traits in southernmost Arctic char populations

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ARTICLE

Elevated temperature and deposited sediment jointly affect early life history traits in southernmost Arctic char populations

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Abstract: The combination of global warming and local stressors can have dramatic consequences on freshwater biota. Sediment deposition is an important pressure that can affect benthic species and benthic ontogenetic stages (eggs and larvae) habitat quality. However, knowledge on the effects of sediment in a warming context is lacking. We used a common garden approach to examine the effects of combined exposure to elevated temperature and deposited sediment on early life history traits in offspring of four wild Arctic char (*Salvelinus alpinus*) populations, originating from geographically isolated lakes at the southern edge of the species range. We report interactive effects of temperature and sediment, with higher temperature exacerbating the negative effects of sediments on the duration of the incubation period and on the body size – yolk expenditure trade-off during development. Our results highlight that reevaluating the impacts of sediment on organisms under the lens of global warming and at the scale of several wild populations is needed to improve our understanding of how vulnerable species can respond to environmental changes.

Résumé : La combinaison du réchauffement planétaire et de facteurs de stress locaux peut avoir des conséquences dramatiques sur le biote d'eau douce. Le dépôt de sédiments exerce une importante pression qui peut avoir une incidence sur les espèces benthiques et la qualité de l'habitat de différents stades ontogénétiques (œufs et larves) d'organismes benthiques. Les connaissances sur les effets des sédiments dans un contexte de réchauffement manquent toutefois. Nous utilisons une approche de jardin commun pour examiner les effets de l'exposition combinée à des températures accrues et à des sédiments sur des caractères des premières étapes du cycle biologique de la progéniture de quatre populations sauvages d'ombles chevaliers (*Salvelinus alpinus*) issus de lacs isolés géographiquement situés à la limite sud de l'aire de répartition de l'espèce. Nous faisons état d'effets interactifs de la température et des sédiments, des températures élevées exacerbant les effets négatifs des sédiments sur la durée de la période d'incubation et sur le compromis entre la taille du corps et l'utilisation du vitellus durant le développement. Nos résultats soulignent le fait qu'il est nécessaire de réévaluer les impacts des sédiments sur les organismes dans une optique du réchauffement planétaire et à l'échelle de plusieurs populations sauvages, afin d'améliorer la compréhension des réactions possibles d'espèces vulnérables aux changements environnementaux. [Traduit par la Rédaction]

Introduction

Temperature elevations induced by global climate change have been challenging the distribution, physiology, and phenology of species (Parmesan 2006; Bellard et al. 2012; Comte and Olden 2016). Additionally, ecosystems ought to cope with a wide array of local pressures. Because of their interactive effects on the system and its communities (Piggott et al. 2015*a*, 2015*b*), multiple stressors have already been acknowledged as one of the causes of the current worldwide decline of freshwater fish populations (I. Côté et al. 2016; Gordon et al. 2018). It is therefore crucial to assess the effects of multiple stressors on biota in a fast-changing climate context, especially on embryo–larval stages that are known to be more sensitive to environmental changes than later life stages (Rombough 1988; Pankhurst and Munday 2011; Lange et al. 2018).

Water temperature and the metabolism, growth, and development rates of fish are firmly linked (Angilletta et al. 2003), thus affecting the life history and fitness of individuals (Zuo et al. 2012; Hemmer-Brepson et al. 2014). Besides, fine sediment (particles of less than 200 μm diameter; Argent and Flebbe 1999) accumulation is an important pressure naturally present in freshwater ecosystems (Townsend et al. 2008). However, both anthropogenic activities (agriculture, urbanization) and natural events (flood

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frequency) can boost sediment input in lakes and rivers (Reid et al. 2018). Once deposited, fine sediment affects habitat structure, food availability, and important ecological processes that can in turn alter the overall ecosystem functionality (e.g., organic matter processing; Piggott et al. 2015b) or trophic relationships (Louhi et al. 2017). Owing to its properties that limit oxygen availability, deposited sediment can exert adverse effects on the embryo survival, development, timing of hatching, and growth of many fish species (see Kemp et al. 2011; Chapman et al. 2014), particularly in salmonids that are highly sensitive to breeding habitat degradation (Greig et al. 2007; Jensen et al. 2009; Louhi et al. 2011; Suttle et al. 2004).

Among at-risk species is the Arctic char (*Salvelinus alpinus*), a cold-water salmonid of cultural and economic importance throughout Northern America and Europe (Klemetsen et al. 2003; Winfield et al. 2018). Distributed across the Northern Hemisphere up to 80°N (Klemetsen 2013), the Arctic char is the northernmost freshwater fish species on the planet and has a limited thermal tolerance range compared with other salmonids (Sæther et al. 2016; Baroudy and Elliott 1994b; Elliott and Elliott 2010). Optimal egg incubation occurs at 4–7 °C (see Sæther et al. 2016; Janhunen et al. 2010), and egg mortality increases dramatically when temperature reaches 8 °C (Jungwirth and Winkler 1984). In Europe, Arctic char populations of the alpine and peri-alpine region are landlocked and located at the southernmost limit of distribution of the species, where embryo–larval life stages already experience temperatures close to their known upper thermal limit of 8 °C (Elliott and Elliott 2010). While adults can migrate in the water column to track more suitable conditions, newly hatched individuals remain within the substratum, exhibiting very limited swimming behavior until they reach the first exogenous feeding stage that follows yolk sac absorption (Wallace and Aasjord 1984; Teletchea and Fontaine 2010). Compared with the pelagic larvae of other freshwater fish species, demersal salmonid embryos remain exposed to sediment for extended periods of time, and might be particularly at risk to its accumulation until hatchlings emerge from the substratum (Sternecker et al. 2013).

Since temperature affects oxygen demand and fine sediment reduces oxygen availability in the environment, it is reasonable to hypothesize these two stressors will interact when experienced in combination, as they both affect energy metabolism in a complementary manner (McBryan et al. 2013; Del Rio et al. 2019) and will likely affect primarily cold-water demersal and benthic species in their embryo–larval stages. In a recent study, Mari et al. (2016) showed that temperature influences negatively fine sediment tolerance of embryos of an Arctic char captive brood stock. Much is known about early development and growth of Arctic char in hatchery settings (Jeuthe et al. 2015; Sæther et al. 2016), but few studies have examined the effects of environmental stressors on early life history traits in natural populations (e.g., Swift 1965; Jungwirth and Winkler 1984; Humpesch 1985). Here, we investigate the combined effects of increased temperature and deposited fine sediment on embryonic life history traits of four wild Arctic char populations located at the southern edge of the species distribution. We conducted a common garden experiment, rearing embryos at either an optimum developmental temperature or at a stressful regime close to their upper thermal limit, and in absence or presence of deposited sediment. As we hypothesized that combined exposure to the stressors would affect early life traits more negatively than when experienced separately, our results provide insights into the sensitivity of early life stages of Arctic char to unfavorable environmental conditions and into the variation in response capacity among wild char populations.

Materials and methods

Ethics statement
This experiment was designed in accordance with the European Directive 2010/63/EU on the protection of animals used for scientific purposes. As this study focused on fish embryos and larvae that rely on endogenous feeding only, no special ethics permission was required. Permission for fish captures on the field was granted by local authorities.

Study populations
We collected spawning individuals in December 2016 and January 2017 from four geographically isolated lakes located around the southern limit of the species distribution range in Europe (Fig. 1A): Lake Geneva and Lake Constance (Switzerland–Germany–Austria), where Arctic char is native, and Lake Pavin (France) and Lake Sainte-Croix, where the species was respectively introduced in 1859 and 1992 from the Lake Geneva population (Machino 1991). In Lake Geneva, allochthonous introductions have been documented in the 1970s, but the population recovered its initial genetic diversity almost entirely today, with no traces of the initial admixture observed (Savary et al. 2017). The Geneva, Constance, and Pavin populations are currently managed through supportive breeding practices, with eggs obtained from local spawners, while the Sainte-Croix population is not managed. These four populations inhabit contrasted thermal habitats, particularly during the egg incubation period, during which average temperatures at spawning ground depths range from 3 °C (Pavin) to 9 °C (Sainte-Croix; Fig. 1B).

Spawner capture and embryo rearing conditions
Spawning adults were caught with gillnets between December 2016 and January 2017 on one spawning ground per lake. Males and females (see online Supplementary Table S1[1]) were crossed to produce 25 independent families in total. Because of limited spawner availability, the number of families produced varied among populations (Pavin: eight families, Constance: five families (three full-sib and two half-sib families), Geneva: six families, Sainte-Croix: six families). All ova were fertilized in the field at water temperatures between 3 and 5° C and brought back to the Institut national de recherche pour l'agriculture, l'alimentation et l'environnement (INRAE) facilities in Thonon-les-Bains, where they were individually distributed into 24-well cell culture microplates (Nunc MicroWell), a now common setup to rear salmonid eggs experimentally and monitor embryonic development at the individual level (Côte et al. 2012; Wilkins et al. 2015).

We set up two sediment treatments (absence — "control" and presence — "sediment exposed"). In a previous study (Mari et al. 2016), we observed significant effects on survival at a minimal sediment load of 0.015 g·cm^{-2} along a gradient of sediment exposure. We selected this load for the exposed treatment in the current study as it represents a low but realistic sedimentation rate (Loizeau et al. 2012) that occurs over the Arctic char egg incubation period in Lake Geneva. We used the same sediment collecting method that is described in Mari et al. (2016). Sediment was collected by pumping water at 51 m deep in Lake Geneva, then mesh-sieved to retain the <200 μm diameter grain-size fraction, known to be the most harmful to fish early life stages (Kjelland et al. 2015). Sediment was oven-dried (60 °C for 72 h) prior to being resuspended in mineral water (Volvic; Mari et al. 2016) to obtain a dilution corresponding to our chosen sediment load. After distributing one egg per microplate well, 2 mL of either clear water or resuspended sediment solution was added to each well of the corresponding microplates. We left sediment to deposit at the bottom of the wells, similarly to the sedimentation process

Fig. 1. (A) Map of the four source lakes from which spawning individuals were caught. The base map image was created with the maps and ggplot2 packages in R and was graphically optimized in PowerPoint. (B) Daily average temperature from November to June in the four source lakes. Lakes Pavin and Geneva temperatures were recorded from December 2015 to May 2016 on Arctic char spawning grounds at 14 and 40 m depth, respectively, using HOBO loggers with one recording every 10 min. Sainte-Croix temperatures were recorded at the lake maximum depth (60.5 m) from November 2015 to June 2016. Lake Constance temperatures were obtained from already available data at depths corresponding to spawning grounds depths (40 m; Limnological Institute of the University of Konstanz). Shaded area in panel B indicates egg incubation period. [Colour online.]
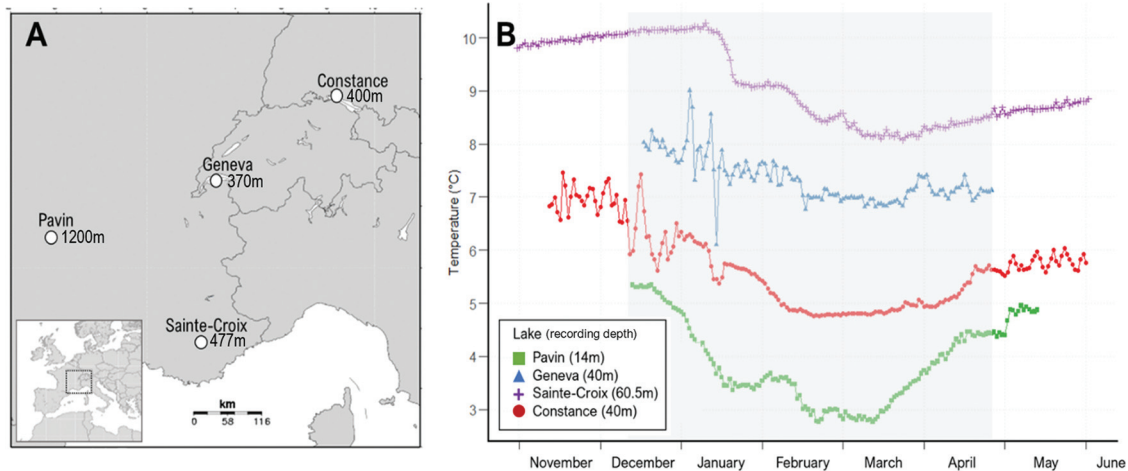
observed in the substratum of spawning areas. Then, plates were split into two batches and incubated in separate climate chambers. In each chamber, plates were randomly distributed on a rack. We set up a cold temperature treatment of 5 ± 0.090 °C, optimal for development, and a warm treatment of 8.5 ± 0.038 °C that is supposedly stressful, but experienced by the species on spawning grounds of Lakes Geneva and Sainte-Croix (Mari et al. 2016). Temperature was recorded from fertilization to hatching using HOBO loggers (HOBO Onset, model No. UX100-001).

We used duplicates of 12 eggs per family per population in plates containing no sediments and triplicates of 12 eggs in sediment plates, as we were expecting higher mortality in sediment-exposed individuals (total of 2640 eggs, two families per plate). For the Sainte-Croix population, sediment effect was tested on three families out of six, because three females produced clutches of fewer than 100 eggs.

Early life trait measurements

Each plate was photographed at the beginning of the experiment (Nikon D5300 and Nikon DX 18–105 mm lens). Individual egg size was measured to the nearest 0.01 mm as the mean diameter (average of two perpendicular diameters) of the egg. Plates were initially left to incubate in the dark so as to not disturb the first stages of development during the first week of incubation and were then monitored daily (every morning) during hatching period. Each newly hatched fish was anaesthetized with 0.35 mL eugenol·L^{-1} (i.e., clove oil diluted 1:10 into 95% ethanol) and photographed individually using the same setup as described above. Body size was measured as the length from the snout to the end of tail (total length in mm, TL), and yolk sac volume (YSV) was calculated using the following formula: YSV = $\pi/6 \times L \times H^2$ (with L = major axis and H = minor axis, in mm; see Kamler 2005). Individual egg size, length, and yolk sac axes at hatching were measured using IMAGEJ (http://rsbweb.nih.gov/ij/download.html). Because sediment-exposed eggs were fully covered by a sediment layer, we could not measure fertilization success and early-life mortality at eyed stage. Thus, survival was estimated as the number of hatched embryos divided by the number of eggs per family. While including unfertilized eggs might bias survivorship rates

downwards, it allows accounting for any mortality that occurred before the eyed stage. However, fertilization success can vary among and within populations. Thus, to allow population comparisons, we standardized survival estimates relative to the trait value in the most optimal environment for egg development, that is, the control (cold, no sediment) treatment as standardized survival = $x_{treatment}/\mu_{control}$, with x being mean survival of a given family; treatment being one of the four treatments (cold, cold exposed, warm, warm exposed); and $\mu_{control}$ being mean survival of a given family in the control treatment. Incubation period was calculated from the number of days from fertilization to hatching as a development rate in accumulated degree days (ADDs): ADD = mean daily temperature × number of days between fertilization and hatching date. ADD represents the heat accumulated by developing embryos until hatching (Crisp 1981) and thus constitute a more biologically relevant metric for incubation duration than days.

Statistical analyses

All analyses were performed using R version 3.6.2 (R Core Team 2019), applying a critical significance threshold of 0.05. We analyzed the relationship between the relative changes in life history trait values and treatments using linear mixed models (LMM and GLMM) with the lme4 package (Bates et al. 2015). We ran one mixed model per trait to test for global effects of treatments, as well as differences among populations. We used a Gaussian error distribution following log transformation to improve normality and homoscedasticity in incubation duration, body size, and YSV models and a binomial distribution for survival model. Temperature and sediment treatments and their interaction and population origin were specified as fixed effects, whereas family identity was set as random effect. Plate identity was set as random effect in all models except survival, because this trait was calculated at the family level instead of individually. Incubation duration was included as a fixed covariate in all body size and YSV models. Owing to the importance of maternal investment in egg size in salmonids (Leblanc et al. 2014; Perry et al. 2005; Polymeropoulos et al. 2016), individual egg size was included as a fixed covariate in all models. All mixed models were fitted under maximum-likelihood

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Table 1. Linear mixed model testing for the overall effects of temperature, sediment exposure, population, and one- and two-way interactions on relative changes in survival, incubation duration, size, and yolk sac volume (YSV) at hatching.

Fixed effects	df	Survival ($n = 2640$) χ^2	p	Incubation ($n = 1540$) χ^2	p	Length ($n = 1540$) χ^2	p	YSV ($n = 1540$) χ^2	p
Temperature	1	32.54	**<0.001**	320.03	**<0.001**	181.01	**<0.001**	19.13	**<0.001**
Sediment load	1	2.22	0.136	0.20	0.655	119.19	**<0.001**	0.74	0.390
Temperature × sediment load	1	3.81	0.051	6.74	**0.009**	14.11	**<0.001**	0.23	0.632
Population	3	16.95	**<0.001**	29.79	**<0.001**	21.23	**<0.001**	14.02	**0.003**
Temperature × population	3	3.93	0.270	20.53	**<0.001**	12.84	**0.005**	32.19	**<0.001**
Sediment load × population	3	5.30	0.506	29.20	**<0.001**	5.99	0.112	10.86	**0.030**
Temperature × sediment × population	3	6.99	0.136	3.54	0.315	1.09	0.780	1.048	0.902
Egg size	1	0.16	0.687	0.17	0.683	48.56	**<0.001**	64.19	**<0.001**
ADD	1	—	—	—	—	72.29	**<0.001**	0.35	0.555

Note: Bold values indicate $p < 0.05$ (likelihood ratio tests). ADD, accumulated degree days.

Fig. 2. Effects of the four treatments on (A) standardized survival rate ($n = 2640$), (B) length of incubation period ($n = 1540$), (C) length at hatching ($n = 1540$), and (D) yolk sac volume (YSV) at hatching ($n = 1540$) for the four study populations. For each treatment, from left to right: blue: Pavin, green: Constance, yellow: Geneva, orange: Sainte-Croix. Values are expressed as mean ± SE. Letters indicate significant post hoc differences between populations within each treatment and between treatments within each population ($p < 0.05$, Benjamini–Hochberg correction). Note that survival is represented here as a rate standardized to the survival rate observed in cold control for clarity, but testing was performed on raw survival data, hence the differences observed among populations in the control treatment. All other traits are represented as raw data. [Colour online.]
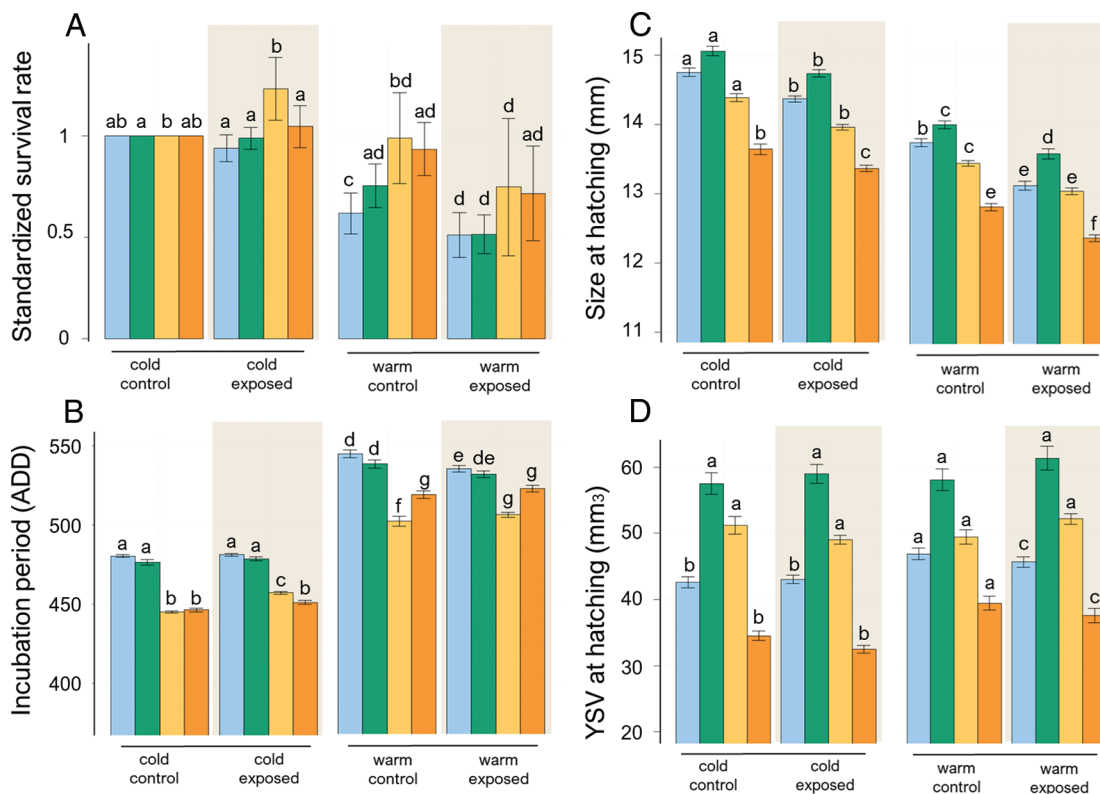
estimation. The significance of independent variable was tested by comparing models including or not including the explanatory variable(s) of interest with likelihood ratio tests, and all residuals for selected models were inspected visually (Q–Q plots) to ensure they did not deviate from assumptions of normality and homoscedasticity. We then performed post hoc multiple pairwise population comparisons in each treatment and between treatments in each population. Pairwise differences were estimated using the emmeans package in R (Lenth et al. 2018), applying a Benjamini–Hochberg correction to account for false discovery rate (Yekutieli and Benjamini 2001).

Results

Effects of temperature and sediment on survival

Overall, temperature had a significant negative effect on survival (Table 1). Post hoc testing revealed significantly lower survival in the Constance and Pavin populations in the warm exposed treatment both with and without sediment (Fig. 2), appearing to be the most affected by warm temperatures during development. Survival declined by 25% and 40%, respectively, when exposed to warmer temperature alone and by 50% for embryos of both origins when exposed to temperature and sediment in combination.

Effects of temperature and sediment on incubation period

Incubation period, measured in ADDs, was significantly longer in the warm treatment for all populations (Table 1). There was no effect of sediment exposure on incubation period overall, but the temperature × sediment interaction was significant. The model showed differences among populations in their responses to temperature and sediment exposure (significant interactions with population; Table 1). The sediment effect was found to significantly increase incubation period in the Geneva population both under cold and warm conditions (significant post hoc testing; Fig. 2). Conversely, we observed a significant decrease in incubation period due to sediment in the warm treatment for the Constance and Pavin populations. This trait was unaffected by sediment in Sainte-Croix individuals. Initial egg size did not have an effect on the duration of the incubation period.

Effects of temperature and sediment on body size and YSV

The size of embryos was influenced by their origin and the temperature experienced throughout development (Table 1). Sediment-exposed individuals were smaller than individuals in the control treatment. Size decreased even more substantially under warm exposed conditions; individuals suffered a 10% reduction in size when they experienced both stressors in combination (compared with control; Fig. 2). Along with a significant temperature × sediment interaction, we detected a significant temperature × population interaction. Body size, length of incubation period, and initial egg size were positively linked. Temperature and sediment together did not affect YSV (Table 1). YSV varied among populations overall and within treatments. Pavin and Sainte-Croix individuals had bigger yolk sacs in the warmer treatment. Sediment exposure had a negative effect on the yolk volume of Sainte-Croix individuals only, observable both at cold and warm conditions (Fig. 2).

Discussion

This study focused on the influence of two major pressures in fresh waters, deposited sediment and increased temperature, on early life stages of southernmost Arctic char populations. It illustrates that (*i*) combined elevated temperatures and sediment-rich waters can affect fitness-related traits interactively and (*ii*) wild alpine *S. alpinus* populations have different susceptibilities to these pressures. Because temperature affects biochemical rates of reactions, it is a crucial parameter for early fish development. Our results reflect trait responses that are typically associated with thermal stress in salmonids, such as reduced size and earlier hatching under warmer conditions (Ojanguren and Braña 2004; J. Côte et al. 2016).

Individuals from the Constance and Geneva populations reared in the warm treatment were smaller but had a YSV similar to that of cold treatment conspecifics. This indicates that part of the yolk reserves were not allocated to growth, likely revealing a physiological stress response (Valdimarsson et al. 2002). When yolk conversion efficiency is lower, growth rates are reduced (Heming 1982; Ojanguren and Braña 2004; Kamler 2008), which could explain the observed smaller size at hatching and changes in yolk reserve expenditure. Sediment effects were less pervasive than temperature effects, and we did not detect any changes in survival. In literature, sediment has been linked with a decrease in embryo survival of other salmonids, such as Atlantic salmon (*Salmo salar*) (Levasseur et al. 2006) and brown trout (*Salmo trutta*) (Sear et al. 2016). It is important to note that the amount of sediment to which embryos were exposed in this experiment was rather low compared with known sedimentation rates (e.g., up to 1 g·cm^{-2}·year^{-1} in Lake Geneva; Loizeau et al. 2012). We deliberately used a low but realistic sediment level because detailed information on the local sedimentation conditions in the other source lakes was not available. However, field observations point at the presence of excess organic matter at the bottom of Lake

Pavin, clogging potential char breeding habitat (Desmolles 2016). Sediment was found to affect size of individuals at hatching but not yolk reserves. Incubation period did not vary significantly with sediment exposure, except in the Geneva population for which hatching was slightly delayed. This pattern is nonetheless consistent with our previous findings on char embryos exposed at a similarly low sediment level (Mari et al. 2016) and with other studies that showed that sediment exposure can negatively affect fish larval development, growth (Greig et al. 2005; Sear et al. 2014; Kjelland et al. 2015), and even metabolic performance (Hess et al. 2015, 2017).

In accordance with our initial hypothesis that sediment would exert more harmful effects on life history traits under warm conditions, we detected sublethal effects of sediment in the warm treatment. The population of origin was an important factor in the response of char embryos to temperature and fine sediment, as population appeared to be a significant variable in all models. Although the magnitude of the response to the two stressors experienced in combination was rather weak, the four populations exhibited distinct response patterns. In the populations in which hatched individuals exhibited bigger yolks (Pavin and Sainte-Croix), hatched embryos were much smaller. Temperature alone affected survival strongly, but temperature and sediment did not show significantly interactive effects on survival. When higher temperature and sediment were experienced simultaneously, incubation was significantly shorter than in the control treatment in days, but not in ADD. Our results further showed that ADD requirements until hatching were population-specific and varied with exposure to temperature, sediment, or both stressors. Hatching might occur earlier to compensate the high metabolic costs of an unfavorable environment (Wedekind and Müller 2005; Storm and Angilletta 2007). As example, Constance individuals hatched at fewer ADDs when exposed to both stressors, compared with their conspecifics exposed to warm temperature only, meaning development was accelerated. Conversely, Geneva individuals hatched at a later age in ADDs. Since the hatching process itself is energetically costly (Kamler 2008), hatching can also be delayed because meeting the energy demand necessary for hatching under warm conditions with limited oxygen availability can be more difficult (McBryan et al. 2013). This will be likely linked to the individuals capacity to partition yolk among different physiological functions (respiratory functions, development, organogenesis, growth) that will lead to the establishment of trade-offs during early life (Stearns 1992; Carlson et al. 2004; Kavanagh et al. 2010). This further suggests other physiological or behavioral alterations that would be relevant to investigate, particularly in regard to how early life exposure to temperature and fine sediment may carry effects into later life stages. However, although oxygen limitation can have severe consequences on embryonic traits of salmonids (Côte et al. 2012; Del Rio et al. 2019; Lavery and Cunjak 2019) and induce immediate and long-lasting alterations in the cardiovascular system of adults (Miller et al. 2011; Johnston et al. 2013; Anttila et al. 2015), evidence regarding consequences of early life hypoxia on adult performance is mixed (Wood et al. 2017), and further studies are needed to characterize the long-term effects of developmental environment on salmonid physiology.

Interactive effects of temperature and sediment were less pronounced than expected based on what was observed previously in a captive char brood stock (Mari et al. 2016), where the two stressors combined had induced a 25% decrease in survival and a much shorter incubation period. Captive brood stocks are generally held in artificial conditions (high water quality, nonstressful temperatures), in which adaptation can occur rapidly (Christie et al. 2012). In the present study, our results indicate that wild populations seem to be better adapted than captive fish to exposure to a low but realistic sediment load. This could potentially raise questions on the consequences of supportive breeding practices on the population's capacity to respond to environmental

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stressors. Considering three out of the four populations studied are managed, future research in this direction would be extremely relevant to help management strategies make informed decisions to maintain wild populations. Salmonid early life is tightly linked to maternal provisioning (Perry et al. 2004; Leblanc et al. 2014), which we took into account as individual egg size in this study, although we did not measure egg quality (e.g., yolk composition). Average egg size varied among populations (Supplementary Fig. S2[1]), which could be due to local conditions, genetic divergence, and (or) differences in individual size, as larger females tend to produce larger eggs (Leblanc et al. 2014). This variation is very likely to have contributed to differences observed among populations in length of incubation period, size at hatching, and YSV in the control treatment. Since yolk reserves constitute the only nutritional source available to embryos, egg size variation could have promoted response variability among and within populations, likely through maternal effects. Maternal investment in egg size is known to influence heavily size and energetic reserves in offspring (as seen in fish (Einum et al. 2002; Régnier et al. 2012) or amphibians (Räsänen et al. 2005)). The crossing design used in the present study was not drawn to disentangle genetic (sire and dam combination) from maternal effects, which were both accounted for under a single random effect (termed family identity; Supplementary Table S3[1]). However, in such a common garden experiment with individual egg size as a covariate in statistical analyses, differences among populations reflect to some extent genetic effects. Among- and within-population variation highlights the existing genetic variability that is the basis for responding adaptively to future environmental changes. Furthermore, since the populations of Geneva, Pavin, and Sainte-Croix have the same genetic background and their divergence occurred recently (i.e., over decades), a larger quantitative genetics crossing design might help to investigate whether the different responses we observed could have emerged from local adaptations to local thermal and sedimentation conditions.

Our results show a limited, but significant, interaction between temperature and fine sediment on early life history traits and highlight the negative effects of increased temperature in offspring of wild salmonid populations, with relevance for the conservation of declining Arctic char populations. The species is known to have a lower thermal tolerance and lower capacity to acclimate to higher temperatures than other salmonids, favoring cold, well-oxygenated water (Baroudy and Elliott 1994a; Elliott and Elliott 2010; Anttila et al. 2015). While environmental conditions in European lakes are changing quickly (Salmaso et al. 2018), adults may be able to seek refugia in deeper waters (Jensen et al. 2017; Jones et al. 2008), and a priority might thus be to maintain good overwintering habitat quality and cold-water refugia. In deep, low-elevation lakes, temperature might exceed Arctic char tolerance threshold levels and induce lethal and sublethal effects on embryos, with implications for later reproductive stages, since elevated temperatures can greatly affect later spawning success and next generation offspring quality (Gillet 1991; Gillet et al. 2011; Jeuthe et al. 2015). In alpine shallow high-elevation lakes, temperature in spawning grounds during egg incubation is several degrees below the stressful condition of 8.5 °C that was tested in the present study. Although mountain lakes are highly vulnerable to climate change, with faster projected warming and reduction of ice and snow cover (Thompson et al. 2005), temperature increases probably do not constitute a critical short-term threat for Arctic char early life stages yet. However, many pressures other than temperature may be of concern in the current multiple stressor context, including suspended sediment that can exert destructive effects on fish (Shrimpton et al. 2007; Berli et al. 2014; Chapman et al. 2014), pollutants, and abiotic pressures such as predation or interspecific competition with native and invasive species (Caudron et al. 2014; Morrissey-McCaffrey et al. 2019), all of which warrant further attention.

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