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# Carryover effects of environmental stressors influence the life performance of brown trout

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## Abstract

Carryover effects of environmental stressors occur when experiences of the environment in earlier life stages or seasons influence the performance of individuals later in life. These can be especially critical for species that have diverse developmental transition periods in their life cycle, such as salmonid fish. Sublethal changes in metabolism, size, or growth experienced in early life stages may have a long-lasting effect on the subsequent life performance of these species, but very few studies have formally tested these changes in relation to environmental stressors. Here, we investigated whether different types of fine sediment result in carryover effects that change the life performance of migratory brown trout. First, we manipulated the early habitat conditions of brown trout through the life stages from egg to fry by incubating them in varying substrate treatments (i.e., gravel without added sediment, gravel with added fine sand, and gravel with added organic matter). Exposure to fine sediment during early development had serious effects on the metabolism, size, escape responses, timing of emergence, and potential survival of early life stages. These carryover effects were persistent and remained present over the critical life shift from relying on parentally provided resources as immobile eggs to independent exogenous feeding as parr. Second, fish were relocated as parr to either their original or different treatment environments and their metabolism, size, and growth were reanalyzed. The effects of environmental stress were observed later in their life cycle when fry from the gravel treatment were relocated to sand or organic-rich treatments. These were found to be significantly smaller in size and had a higher metabolic rate than fry maintained in their original treatment environment. Together, our study experimentally demonstrated that the carryover effects of environmental stressors experienced in early stages may influence the fitness outcomes of migratory fish later in life. We suggest that sublethal environmental stressors should be better considered in restoration schemes and management strategies to reverse the current trend of declining salmonid populations.

**KEYWORDS**
brown trout, carryover effects, environmental stressors, escape responses, fine sediment, metabolism

## INTRODUCTION

Species with diverse developmental transition periods in their life cycle may encounter a different environment when they progress from one stage to the next. As their development does not usually reset entirely during these transitions, the environment experienced early in life can influence an organism's survival and reproduction in subsequent life stages, a phenomenon known as "carryover" (O'Connor et al., 2014) or "knock-on" (Jonsson & Jonsson, 2019) effects. Phenotypic plasticity, that is, the ability of individual genotypes to produce altered phenotypes when exposed to different environmental conditions (Jonsson et al., 2022), is gaining increasing interest as the climate is changing faster than ever before (IPCC, 2021), since the ability of species to survive partly depends on their phenotypic and genetic responses to change (Jonsson et al., 2022).

Carryover effects have been demonstrated to exist in multiple organisms and in response to various environmental stressors. They have often been described in ectothermic fish (Jonsson & Jonsson, 2019), in which increased temperatures and low environmental $O_2$ conditions (i.e., hypoxia) affect their aerobic metabolism (Anttila et al., 2015), and their ability to acclimate is related to both stressors: fish increase their metabolism under raised temperatures, and this results in a higher $O_2$ demand. However, the $O_2$ supply might be limited under hypoxic conditions in water, typically caused by excessive nutrient or sediment loading from the watershed and the inverse relationship between oxygen solubility and temperature. Recently, variation in embryonic thermal conditions was inversely related to the metabolic rate of brown trout (*Salmo trutta*) juveniles (Durtsche et al., 2021). Moreover, warm-incubated brown trout eggs produced juveniles that migrated in higher proportions than cold-incubated individuals (Jonsson & Greenberg, 2021). Temperature has also been reported to reduce the growth rate of sea bass (*Dicentrarchus labrax*; Cadiz, Zambonino-Infante, et al., 2018), and hypoxia itself has been related to the prevalence of opercular abnormalities in this species (Cadiz, Ernande, et al., 2018). Exposing brown trout eggs to a low oxygen content in the laboratory delayed the emergence of alevins from the gravel nest (Johnston et al., 2013; Roussel, 2007). Alevins are able to adjust the timing of their emergence in response to environmental factors such as chemical cues from predators (Jones et al., 2003), but the advantage gained through timing and predator avoidance in such a trade-off situation can be obscured by excessive sedimentation (Louhi et al., 2011). Both stressors were also reported to individually affect the metabolism, growth, and developmental rate of Chinook salmon eggs (*Oncorhynchus tshawytscha*; Del Rio et al., 2021).

Salmonid fish are highly sensitive to environmental disturbance, and they are often considered as indicator species in assessing the ecological integrity and quality of rivers (Pont et al., 2006; Welcomme et al., 2006). They also have discrete developmental transition periods in their early life in freshwater (sensu Allan & Ritter, 1977; Elliott, 1994): fertilized eggs develop in gravel beds, where they hatch into alevins, but they remain in the gravel bed after hatching, relying on parentally provided resources and feeding on their yolk sac. After this, they undergo a critical life stage shift and emerge from the gravel as fry, start their independent exogenous feeding and dispersal, and finally become parr once they have fully absorbed their yolk sac. Human-induced sedimentation has the potential to affect all factors that their survival depends on, such as growth, reproduction, finding food, and avoiding predators (e.g., Kemp et al., 2011; Skoglund et al., 2011). Hypoxia also has detrimental effects on sensory performance and the neural control of escape performance in fish (Domenici et al., 2019). The responsiveness and timing of the response (i.e., latency time) are the key variables that determine the success of fish in escaping from predators (Fuiman et al., 2006), but to our knowledge, no information exists on the effects of sedimentation in the embryonic stage on the escape responses of salmonids. Thus, they provide an ideal vertebrate species group for investigating the carryover effects of an environmental stressor, such as sedimentation, on their early life.

Increased surface runoff increases the transportation of sediment into river systems, posing a threat to freshwater species (Murdoch et al., 2020; Piggott et al., 2015), particularly to life stages that are unable to relocate to more favorable environments. Sedimentation is a common stressor within natural salmon redds; it reduces the circulation of water in the gravel bed and hence oxygen availability, or physically prevents the fry from emerging from the gravel bed. The direct effects of suspended and deposited fine sediment on the early life stages of salmonids are relatively well known (most recently reviewed by

Smialek et al., 2021). However, evidence for the deleterious carryover effects of embryonic oxygen depletion or a simplified habitat caused by sedimentation is scarce.

Here, we focused on the carryover effects of excessive sedimentation on the early life stages of brown trout in a multiphase experiment. First, we experimentally tested the influence of fine sediments (organic matter [OM] and inorganic sand, both <2.0 mm in diameter) on the metabolic rate ($MO_2$), size, emergence, escape responses, and survival of the relevant brown trout embryonic stage (egg, alevin, or fry) in indoor experimental channels. Second, we mimicked the movements of parr to a more suitable habitat if available in natural rivers and transported parr to either their original or different treatments in outdoor experimental channels and remeasured their metabolic rate and size. As parr, salmonids establish and defend their feeding territories in the river. If river habitats are aggraded in a patchy distribution, salmonids often swim to find a more suitable habitat (Sullivan & Watzin, 2010), but if the spatial distribution of sediments is more uniform, adverse effects via habitat alterations may be spread across multiple life stages (e.g., adults, nest building, egg development and fry feeding) (Newcombe & Jensen, 1996). We hypothesized that both sand and OM have detrimental but varying effects on response variables, and these were expected to remain present over the critical life stage as an expression of the carryover effects of environmental stressors. OM in particular was expected to cause a slower metabolic rate and development in the egg-to-fry-phase due to its oxygen-consuming decomposition that may lead to hypoxic environment. The importance of sand was expected to increase in the fry-to-parr-phase, as sand can block the pores of the gravel bed and reduce the complexity of the habitat and availability of shelter, specifically affecting juvenile fish (Finstad et al., 2007). These effects were expected to be detected as an increased metabolic rate and smaller size of parr.

# METHODS

## Site description and experiment design

The multiphase experiment (Figure 1) was conducted at the facilities of Kainuu Fisheries Research Station (Natural Resources Institute Finland, Paltamo) from 16 October 2018 to 3 July 2019. To assess whether the metabolic rate ($MO_2$), escape response, size, and survival to emergence of brown trout were affected by sediment, we applied a randomized factorial design with three sedimentation treatments (gravel with no added sediment, with added sand, and with added OM), with three replicates per treatment (Phase 1). The experimental facilities were the same as described in detail in Louhi et al. (2011). Thus, only a brief summary of the facilities is provided here, and our focus is on the implemented measurements. The experiment was continued until the parr stage in outdoor experimental channels with either the original treatment or a "crossed" treatment, that is, transfer from one of the three treatments to another, with three replicate boxes for each treatment combination (described in detail in the section *Phase 2: Outdoor experimental arena for early parr*).

The parameters were measured in four stages: (1) as eyed eggs (~381 degree-days, 21–24 January; Phase 1); (2) as recently hatched alevins (~489 degree-days, 18–22 February; Phase 1); (3) after the onset of fry emergence (~763 degree-days, 23 April–6 May; Phase 1); and (4) as early parr (24 June–3 July; Phase 2). All experiments were carried out under a license obtained from the Finnish National Animal Experiment Board (ESAVI/2175/2019).

## Phase 1: Indoor experimental arena from egg to fry emergence

The experimental channels, arrangement of water flow, and artificial light regime were similar to those described in Louhi et al. (2011), except for some practical rearrangement of channel positioning due to the lower number of channels used in this experiment. Three sedimentation treatments were randomized across the nine channels, and three 1-L plastic circular cylinders (diameter 8 cm and height 18 cm) containing brown trout eggs were buried flush into each channel on 16 October. The eggs for the experiment were obtained from 18 female brown trout that had been fertilized with sperm pooled from 18 males from the same stock to randomize the genetic variation (Bloomer et al., 2018). After fertilization, the eggs were immediately water-hardened for 16 h at 7.0°C. Within 24 h of fertilization, 100 eggs were evenly deposited among washed gravel (8–32 mm) in each cylinder. All eggs used in the experiment were of the same initial size (mean diameter $5.5 \pm 0.3$ mm, $n = 100$). Throughout Phase 1, all channels received an individual but similar inflow, which was set at $1.65 \pm 0.05$ L $min^{-1}$. The water temperature followed the natural temperature of lake water, ranging from 3.9 to 10.5°C during Phase 1 (~8 months, 962 degree-days in total).

Fine sediment (120 ml) was added weekly into specified channels from the start of the experiment until the first measurements. For sediment additions, sieved fine sand collected from a nearby sandpit and organic matter

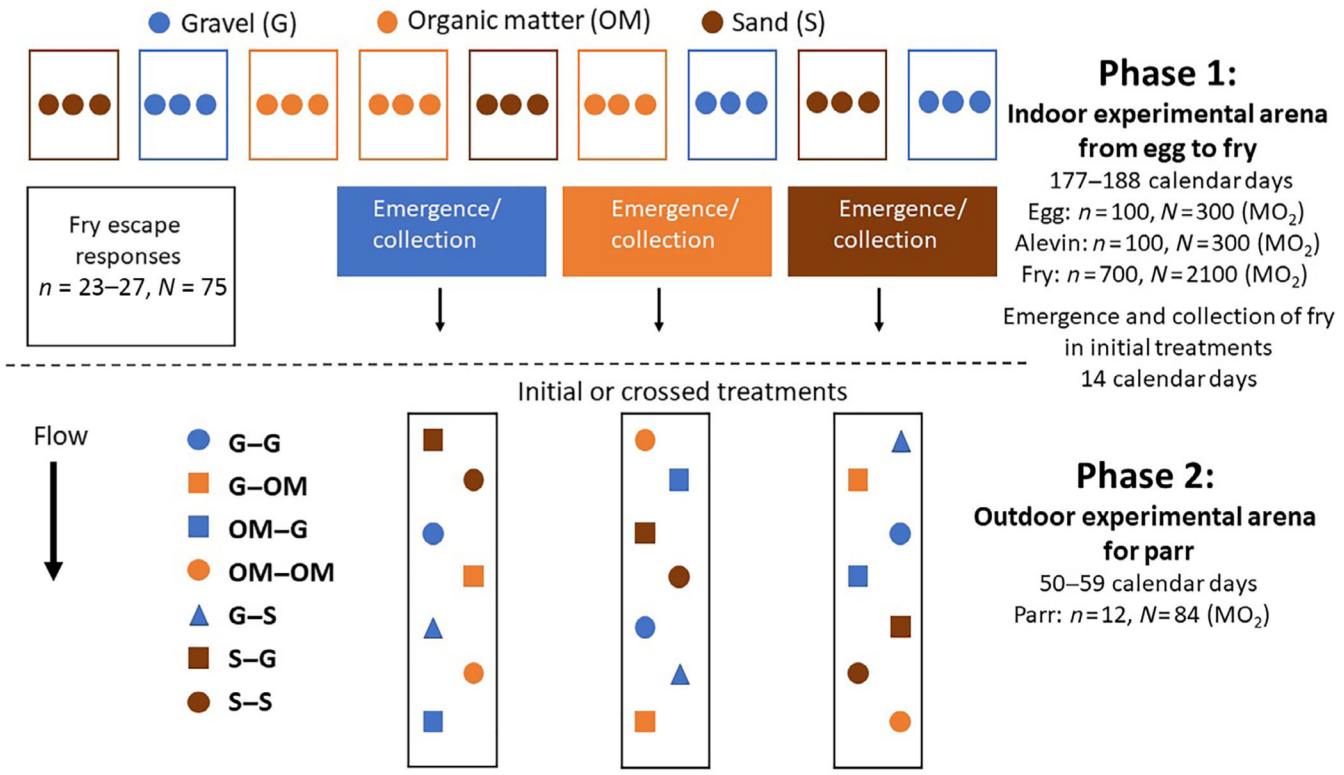


**FIGURE 1** Schematic presentation of the multiphase experiment design. In Phase 1, brown trout eggs and alevins were incubated in cylinders inside randomly ordered channels in three treatments (three replicate boxes for each): (1) gravel without added sediment (blue circles), (2) gravel with added organic matter (orange circles), and (3) gravel with added fine sand (brown circles). Escape responses were individually measured from 23 to 27 fry per treatment, while other fry were collected and held under similar conditions before being randomly placed (four fish in each box) in "original" or "crossed" treatments set in flow-through boxes inside outdoor channels (Phase 2; seven treatments, three replicate boxes for each treatment combination). The original treatments (treatment in Phase 1 followed by Phase 2) were as follows: blue circle G–G: gravel–gravel; orange circle OM–OM: organic matter–organic matter; brown circle S–S: sand–sand. The crossed treatments were as follows: orange square G–OM: gravel–organic matter; blue square OM–G: organic matter–gravel; blue triangle G–S: gravel–sand; brown square S–G: sand–gravel. Parameters other than escape responses were measured in four stages: egg, alevin, fry, and parr. The numbers of replicates (*n*: per treatment; *N*: all in a particular stage) and the duration of phases in calendar days are given on the right (see Appendix S1: Table S2 for details).

(diameter < 2.0 mm for both) collected from a nearby peatland were used. The mean mass of deposited sediment in both sand and OM treatments differed significantly from channels without additions by the end of Phase 1 (Appendix S1: Table S1).

The number of living eggs ($n = 100$ eggs) and alevins ($n = 100$ eggs) was counted from one cylinder per treatment immediately after their removal from the gravel and used for measurements of metabolic rate (see section *Measurement of metabolic rate during Phases 1 and 2* below). The survival of emerging fry was recorded from all remaining cylinders ($n = 700$ eggs per treatment). The interstitial oxygen content (in percentage) in the gravel bed was measured from four points (upstream and downstream ends, and both sides) in each channel before the removal of the cylinder using a FiBox 3 fiber-optic oxygen meter (PreSens, Regensburg, Germany).

Just before the expected onset of emergence, a small metal mesh (diameter: 2 mm) was placed on top of the gravel inside each cylinder. The mesh was tight with the walls of the cylinders but had a hole (diameter: 8 mm) in the middle of it to ensure the free emergence of fry from the gravel, and also to prevent them from re-burrowing after their first appearance. No re-burrowing or other difficulties in emergence were noticed. Once emergence began, each cylinder was checked daily and emerged fry were moved to mesh boxes ($10 \times 30 \times 8$ cm) resembling their initial treatments inside standard rearing tanks until continuing to Phase 2 of the experiment. The water temperature was 4.0°C when the first alevins emerged and 4.1°C during the median time of emergence. The emergence period was considered to have ceased when no new fish had emerged for two successive days.

The content of deposited sediment was measured at the end of Phase 1. The remaining cylinders from each channel were carefully removed and quickly placed into a bucket. Some sediment may have been lost during this operation, but as the procedure was similar for all cylinders, this should not have created bias in the treatment comparisons. In the laboratory, all gravel was carefully removed by flushing the contents of the cylinders, and the remaining sediment was oven-dried (105°C) for 12 h. Fine sediment (<0.7 mm) was separated from the rest of the sediment by sieving, and the inorganic and organic contents were then measured through combustion at 550°C for 6 h. Note that the research station was supplied with water from a lake, so all treatments received a small but equal amount of natural organic matter (chemical oxygen demand, $COD_{Mn}$, 11 mg $L^{-1}$; Hertta 5.7. Open Data Source, 2019). The levels of sedimentation in the experiment corresponded well with the amount observed in streams that drain forestry-impacted catchments (Appendix S1: Table S1; Louhi et al., 2010).

## Phase 1: Escape response experiment

The experimental setup consisted of a white plastic tank (35 × 43 cm in diameter, 6 cm water depth, water volume 9 L). In the middle of the tank, a metal mesh cylinder (mesh size 2 mm, diameter 30 × 7 cm height) was secured on the bottom. The water temperature was maintained at a mean of 4.2°C (range 3.6–4.5°C) throughout the experimental period (12 days). For the escape response experiment, one fry from each treatment ($n = 23$–27 per treatment) was transferred to the middle of a circular arena and allowed to acclimate for at least 30 min (Appendix S1: Table S2). To induce an escape response, a metal ball (50 g) attached to a fishing line was released like a pendulum from a stand set by the side of the tank (fixed height was 140 cm, release angle was 30°, and release distance from the tank was 73 cm). The tank and the stand were shielded with a black plastic sheet, so fish were unable to see and/or sense either the approaching stimulus or the person releasing the ball. The escape response of each fish was recorded at 500 fps (frames per second) with a high-speed camera (Sony DSC-Rx100MarkVI, Sony, Tokyo, Japan) placed above the tank. The experimental arena was illuminated using a GODOX LEDP120C led panel light (GODOX Photo Equipment, Shenzhen, China). The videos of the escape responses were analyzed frame by frame using Tracker Video Analysis and Modeling Tool 5.0.7 (Brown & Hanson, 2020).

The nonlocomotor variables were analyzed following the study of Marras et al. (2011): (1) responsiveness, defined as the percentage of fish responding to the stimulation with an escape response; (2) the mean, maximum, and minimum escape latency time (in milliseconds), defined as the time between the ball hitting the side of the tank and the first detectable movement of the fish head; and (3) the escape type, defined as either a single bend (SB) or double bend (DB). The escape response consists of an initial unilateral muscular contraction (stage 1), which is usually followed by a second contralateral contraction (stage 2) corresponding to the main propulsive thrust (Domenici & Blake, 1997). The escape type was defined as SB if only stage 1 was present and DB when it was followed by stage 2.

## Phase 2: Outdoor experimental arena for early parr

Phase 2 of the experiment was conducted in three 25 × 1.5 m parallel outdoor channels with concrete walls and bottoms covered by a 15-cm layer of gravel-to-pebble-sized particles (8–50 mm in diameter). The treatments resembled Phase 1, as the sand treatment received 6 L of fine sand and the OM treatment received 5 L of the same organic matter as used earlier, which resulted in ~80% coverage in both treatments. No sediment was added into the gravel treatment. Water drained into the channels from a nearby lake (the same as in Phase 1); it then entered a 30-m-long stream section before draining into the experimental arena. Seven plastic flow-through boxes (size of 80 × 60 × 45 cm and water surface area of 0.48 $m^2$ in each) were placed one after another in each channel, and on alternating sides within a channel. The boxes had mesh (Ø 2 mm) on their upper and lower ends parallel to the flow, allowing continuous water flow through them, so no extra food was provided to the fish. Water flow into the channels was adjusted so that all boxes had a similar flow velocity (0.15–0.25 m $s^{-1}$) and water depth (10–15 cm). All boxes were covered with nets during the experiment, resulting in approximately 60% shading. Four parr were randomly placed into each box, either according to their initial treatments (i.e., gravel–gravel [G–G], sand–sand [S–S], and organic matter–organic matter [OM–OM]) or "crossed" treatments (i.e., sand–gravel [S–G], OM–gravel [OM–G], gravel–sand [G–S], and gravel–OM [G–OM]). The design of the outdoor experiment thus consisted of seven treatments with three replicate boxes for each treatment combination.

## Measurement of metabolic rate during Phases 1 and 2

The metabolic rate was measured for eyed eggs, recently hatched alevins, recently emerged fry, and early parr

(Appendix S1: Table S2). The routine metabolic rate (RMR) of eggs and alevins was measured using a Loligo 24-channel optical fluorescence, oxygen-sensing microplate (Loligo Systems, Viborg, Denmark) connected to a sensor dish reader (SDR) (PreSens Precision Sensing, Resenburg, Germany). The eggs/alevins ($n = 20$ per treatment) were placed in 2700-µl wells filled with air-saturated water from fish tanks. Thereafter, the wells were sealed. The measuring system was inside a 40-L water bath that kept the temperature of the water constant and at the temperature of the tanks (3.9°C for eggs and 4.1°C for alevins). In each measuring set, four wells were left empty to monitor the background oxygen consumption rate. The reduction in the oxygen level in wells was recorded with SDR v4.0.0 software (PreSens). The measurements were ended when the oxygen level in wells reached 75% of oxygen saturation. The metabolic rate (in milligrams of oxygen per hour per kilogram) was calculated as follows:

$$MO_2 = ((a - b) \times V_{\text{eff}} \times \beta)/m,$$

where $a$ is the slope of the decrease in the water oxygen level in a well over time (in kilopascals per hour), $b$ is the slope of the bacterial oxygen consumption rate over time (in kilopascals per hour), $V_{\text{eff}}$ is the volume of the well minus the volume of the fish (in liters), β is the solubility of $O_2$ (in milligrams of oxygen per liter per kilopascal), and $m$ is the mass of the fish (in kilograms). A measurement was excluded from the data if the $R^2$ value was below 0.95 or the wells contained air bubbles.

Automatic intermittent-flow respirometry was used to measure both the maximum metabolic rate (MMR) and standard metabolic rate (SMR) of fry ($n = 10$–12 per group) and early parr ($n = 5$–7 per group) according to Svendsen et al. (2016). Fish were directly moved from the outdoor boxes to respirometry to avoid additional handling stress. The size of the measuring chambers was 6.8 ± 0.02 ml for fry and 34.2 ± 0.2 ml for parr. To measure MMR, the fish were manually chased until exhaustion for 10 min. The fish were then rapidly transferred to the chambers, ensuring that no air bubbles were introduced. The chambers were inside a 40-L water bath that continuously received fresh water from the research station, keeping the oxygen levels high for flushing of the chambers between measuring cycles, and the water temperature was kept constant for the whole experiment (4.2 ± 0.1°C for fry and 16.2 ± 0.1°C for parr). The oxygen consumption rates of the fish (four fish were measured simultaneously) were determined with AquaResp software (Svendsen et al., 2019) using Robust Oxygen Probes (Pyroscience, Aachen, Germany). The water inside the chambers was circulated with magnetic stirrers and the flushing between measuring cycles was conducted with an aquarium pump (EHEIM, Deizisau, Germany). For MMR measurement, the respirometry cycles were 330 s in closed mode (30 s for wait and 300 s for measurement) and 30 s in open mode (chamber flushing). The MMR measurements continued for 1 h (12 measurement cycles) and the highest value obtained during that period was used to estimate MMR. SMR measurements directly followed the MMR measurements so that the cycling was changed to 630 s in closed mode (30 s wait and 600 s for measurement) and 120 s of chamber flushing. The SMR measurements lasted 23 h (approximately 100 measuring cycles). During the measurements, the setup was covered with a black plastic sheet to avoid any external disturbance. SMR was calculated as the mean of the lowest 10 $MO_2$ values after removing the lowest 2% of the dataset (Chabot et al., 2016). The oxygen level never dropped below 75% during measurements and the single measurement slopes that had an $R^2$ value below 0.95 were removed from the dataset. After the SMR measurements, fish were removed from chambers and the chambers were again sealed to measure the background bacterial $MO_2$ (flush time was 30 s and measurement time was 1800 s). The system was cleaned with 10% bleach solution after each measurement set to ensure that bacteria would not start growing in the chambers and tubing. The $MO_2$ values were calculated using the same formula as presented above. The aerobic scope (AS) was calculated as the difference between SMR and MMR.

## Fish size measurements in Phases 1 and 2

After each stage of the experiment, the fish were measured (Appendix S1: Table S2). The diameter of eggs was measured with a caliper, and eggs and alevins were then weighed to the nearest 0.1 mg after the metabolic rate measurements. The mass of fry and early parr was determined before the $MO_2$ measurements. Alevins, fry, and early parr were also photographed individually (Sony DSC—HX100V, Sony, Tokyo, Japan) from their sides and above. The alevins, fry, and early parr were anesthetized with benzocaine prior to photographing. Apart from parr, the total length of the fish and size of the yolk sac (yolk-sac area as seen from the side) were measured to the nearest 0.1 mm from the photographs using Fiji software (ImageJ; Rasband, 2018; Schindelin et al., 2012). The total length and mass of parr were measured using standard measuring scales, and the standardized mass-specific growth rate was calculated following Ostrovsky (1995).

## Statistical analysis

The effects of sedimentation treatment (addition of sand or OM) on the size (mass, total length, and growth rate), metabolism (RMR/SMR, MMR, AS, and yolk-sac size), and nonlocomotor variables of escape responses (responsiveness and latency time) in each developmental stage (egg, alevin, fry, and early parr) were analyzed statistically using R statistical software (v. 3.6.0).

In Phase 1, generalized linear models (GLMs) with treatment as the only fixed variable were fitted with the function "glm" for eggs and alevins, as they were sampled separately from one box per treatment, that is, one box was sampled in the egg stage and another one in the alevin stage. For fry, generalized linear mixed models (GLMMs) were fitted, including treatments as a fixed factor and channels and incubation cylinders within channels as random effects in the model (LMM; function "lme" in the package nlme; Pinheiro et al., 2017). When analyzing the number of emerging fry and their size measurements (mass, length, and yolk-sac area) between treatments, the number of days since the beginning of emergence was also included as a random factor in the models to control for the potential confounding effect of time. The residuals were graphically inspected and found to satisfy the assumptions for the models, and the results are presented as treatment contrasts.

As data exploration also revealed potentially significant nonlinear relationships between the response and explanatory variables outside the set treatments, generalized additive modeling (GAM) was performed to assess the relationship between egg-to-emergence survival, total length, mass, yolk-sac size, SMR, MMR, and organic and inorganic sediment using the mgcv package (Wood, 2021) for R statistical software. The initial full models included the main effects of sediments with a smoothing term as fixed effects and the cylinders nested within channels as random effects. The selection of the optimal model for response variables, $S_{ij}$ (in the $i$-th cylinder in the $j$-th channel), resulted in a model that included the effect of sediment (SED) as a fixed effect and no random effects ($p > 0.05$). Thus, our final model was as follows:

$$S_{ij} = \beta_0 + \mathrm{F}(\mathrm{SED}_{ij}) + \varepsilon.$$

In Phase 2, the analyses followed a similar logic to Phase 1, and the results are given as treatment contrasts, but we focused on significant comparisons between the same or crossed treatments in the fry and parr stages (i.e., gravel–gravel vs. gravel–OM or gravel–sand, OM–OM vs. OM–gravel, and sand–sand vs. sand–gravel). Comparisons between crossed treatments were assumed to indicate a potential difference between no changes at all in their habitat and relocating themselves after a stationary incubation period to a more suitable habitat. In these models, the channels and boxes within them were included as random effects.

# RESULTS

## Phase 1: Egg to fry stages

The highest survival rate of eggs was in gravel, the next highest was in OM, and the lowest was in the sand treatment (Appendix S1: Table S2). The highest oxygen saturation in gravels around the incubation cylinders was measured in the gravel treatment. No significant differences were observed in the size of eggs (GLM: all $p$ values >0.426 for both mass and volume of eggs). The RMR of eggs was significantly lower in the OM treatment (GLM estimate ± 1 SE: $-12.94 \pm 5.68$, $t = -2.27$, $p = 0.027$) compared with gravel, but showed no significant difference from the sand treatment (GLM estimate ± 1 SE: $-4.80 \pm 7.22$, $t = -0.67$, $p = 0.509$).

By the time the developing eggs reached the alevin stage, survival was highest in the OM treatment, in which the lowest oxygen saturation was measured. Survival and oxygen saturation were at approximately the same level in both the sand and gravel treatments (Appendix S1: Table S2). Alevins in the OM treatment were significantly longer (measured from all living alevins, $n = 78$, GLM estimate ± 1 SE: $0.06 \pm 0.03$, $t = 2.17$, $p = 0.033$) and had a larger yolk-sac area ($0.02 \pm 0.01$, $t = 0.02$, $p = 0.048$) than alevins in the gravel treatment. They were also significantly longer ($0.11 \pm 0.04$, $t = 2.97$, $p = 0.004$) than alevins developing in the sand treatment. No significant differences in RMR, MMR, or AS were observed among the treatments in this phase of development.

The first fry of the experiment emerged from the sand treatment, followed by fry from the gravel and then the OM treatment (Appendix S1: Table S2). The duration of the emergence period was clearly longest in the sand treatment, being 49 days, whereas there was only a one-day difference in duration between the gravel and OM treatments, which were 32 and 33 days, respectively. The relative survival of emerged fry was highest in the OM treatment, being 39% (Appendix S1: Table S2), but no significant difference in the survival of emerged fry was recorded among the other treatments (33% in gravel and 32% in sand; all $p$ values >0.192). The yolk-sac area of fry emerging from OM was marginally significantly smaller compared with fry emerging from gravel (estimate ± 1 SE: $-0.69 \pm 0.40$, $t = -1.71$, $p = 0.089$). No other significant differences in size measurements were

noticed. In addition, SMR, MMR, and AS did not differ significantly among treatments in this phase of development.

The results from the GAM as a function of fine organic sediment (smoothing term) were statistically significant for egg-to-emergence survival ($p = 0.024$, $F_{edf4.97} = 3.45$; Figure 2A), total length ($p = 0.019$, $F_{edf7.42} = 3.66$; Figure 2B), and mass ($p \ll 0.001$, $F_{edf4.10} = 7.68$; Figure 2D). Regarding the size yolk sac, a difference was detected at the 0.07 level ($p = 0.064$, $F_{edf3.88} = 2.74$; Figure 2C). The results also yielded a significant function for MMR ($p = 0.004$, $F_{edf5.47} = 5.05$; Figure 2E) and SMR ($p = 0.013$, $F_{edf2.31} = 5.06$; Figure 2F). No significant relationships between inorganic sediment and response variables were recorded (all $p$ values >0.13), so they are not reported here in any detail.

All but three of the 75 analyzed fry employed the double-bend fast start as an escape response (Appendix S1: Table S2). Interestingly, the fry in the sand treatment reacted significantly less often than those in the gravel (estimate ± 1 SE: −0.09 ± 0.03, $t = -3.18$, $p = 0.005$) and OM (estimate ± 1 SE: −0.11 ± 0.03, $t = -4.20$, $p < 0.001$) treatments (Figure 3A). Moreover, the mean and minimum latency times of fry in the sand treatment were significantly longer than in the gravel treatment (estimate ± 1 SE: 2.52 ± 1.14, $t = 2.21$, $p = 0.041$; estimate ± 1 SE: 1.81 ± 0.85, $t = 2.12$, $p = 0.048$ respectively), but a significant difference in the maximum was only detected at the 0.07 level (estimate ± 1 SE: 10.89 ± 5.40, $t = 2.02$, $p = 0.059$; Figure 3B).

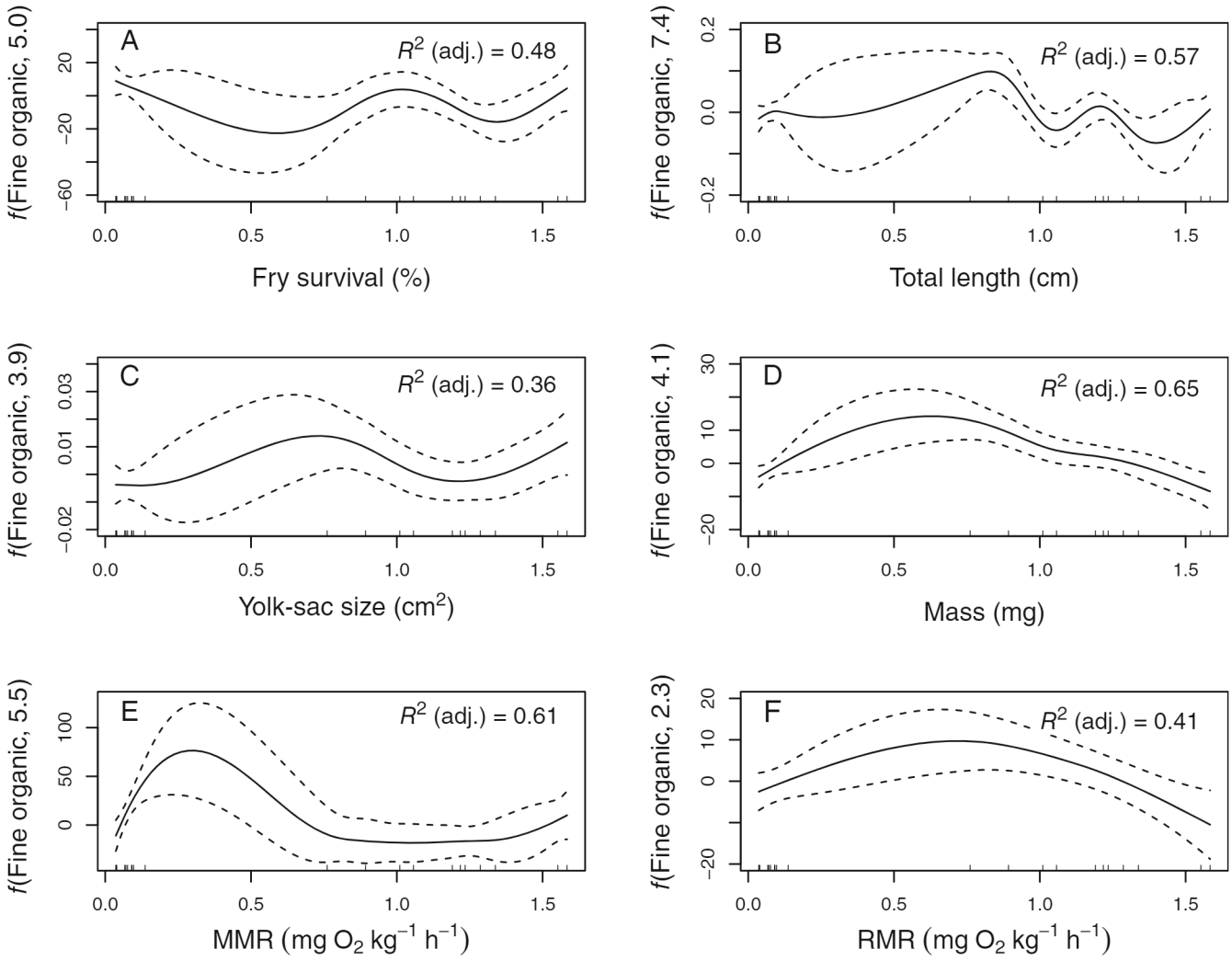


**FIGURE 2** Relationship and effective degrees of freedom estimated from generalized additive models of fine organic sediment and (A) fry survival, (B) total length, (C) yolk-sac size, (D) mass, (E) maximum metabolic rate (MMR), and (F) routine metabolic rate (RMR). The solid line represents the estimated smoothing term (fine organic sediment) for the additive model of the response variables and dashed lines are 95% confidence intervals illustrating the distribution of the data, which are combined across all sedimentation levels. Note the differences between subfigures in the vertical axis.

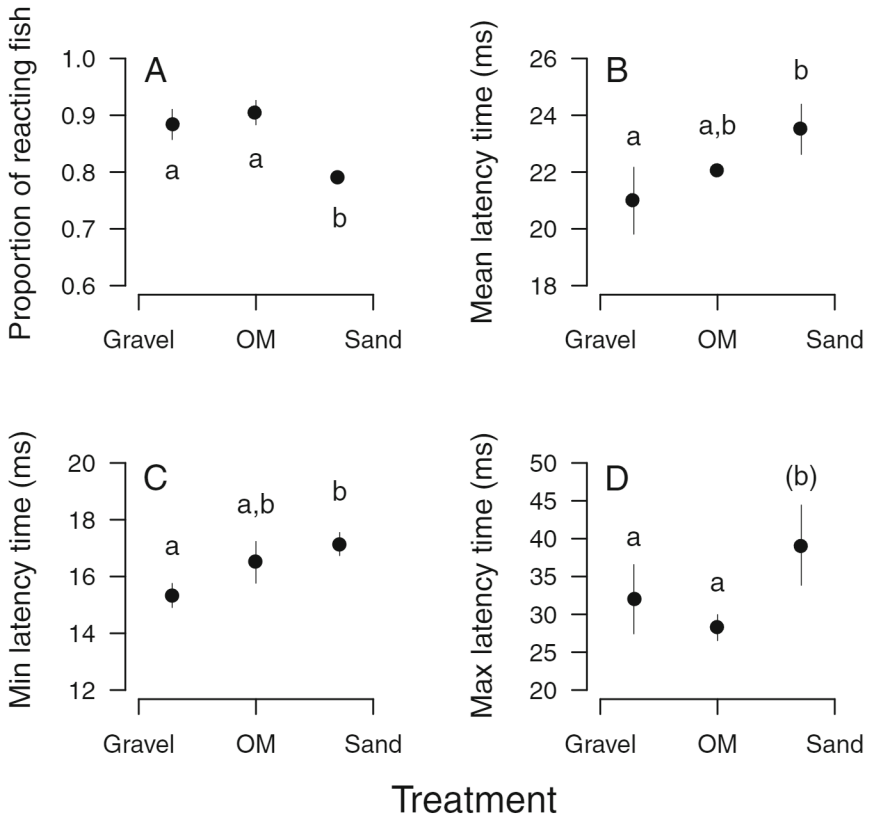


**FIGURE 3** (A) Mean (±1 SE) proportion of reacting fish, (B) mean estimate (in milliseconds) of the latency time, (C) minimum (Min) estimate of the latency time, and (D) maximum (Max) estimate of the latency time in each treatment (gravel, OM = organic matter, sand). Treatments not sharing the same letter differ significantly ($p < 0.05$), and a difference was detected at the 0.07 level when letters are in parentheses.

## Phase 2: Parr stage

Brown trout parr initially maintained in the gravel treatment and moved to the OM treatment (G–OM) in the parr stage tended to have a higher SMR (GLMM estimate ± 1 SE: 35.94 ± 17.04, $t_{13} = 2.11$, $p = 0.055$; Figure 4A), had a significantly lower mass (estimate ± 1 SE: −607.6 ± 206.61, $t_{13} = 2.94$, $p = 0.012$; Figure 5A), and tended to be shorter (GLMM estimate ± 1 SE: −0.52 ± 0.23, $t_{13} = -1.93$, $p = 0.075$; Figure 5B) than parr remaining in gravel treatment (G–G) throughout the experiment. This was confirmed by a similar tendency for the growth rate (estimate ± 1 SE: −3.50 ± 1.64, $t_{11} = -2.14$, $p = 0.055$; no figure shown). Similarly, parr initially maintained in the gravel treatment and moved in the parr stage to the sand treatment (G–S) had a significantly higher SMR (estimate ± 1 SE: 42.85 ± 18.08, $t_{16} = 2.37$, $p = 0.031$; Figure 4A), a lower mass (estimate ± 1 SE: −474.4 ± 206.61, $t_{18} = 2.30$, $p = 0.034$; Figure 5A), and tended to have a lower growth rate (estimate ± 1 SE: −2.77 ± 1.31, $t_{11} = -1.89$, $p = 0.085$) when compared with parr remaining in the gravel treatment (G–G).

No significant differences in SMR, MMM, or AS were detected in parr initially maintained in the OM treatment and moved in the parr stage to the gravel treatment (OM–G; Figure 4A–C). However, they had a significantly higher mass (estimate ± 1 SE: 718.67 ± 197.81, $t_{13} = 3.62$, $p = 0.003$; Figure 5A) and they were significantly longer (estimate ± 1 SE: 0.64 ± 0.26, $t_{13} = 2.48$, $p = 0.027$; Figure 5B), and thus had a higher growth rate (estimate ± 1 SE: 3.73 ± 1.46, $t_{11} = 2.55$, $p = 0.027$) than parr remaining in the OM treatment (OM–OM). Parr moved from the gravel treatment to the OM treatment, however, displayed a tendency for a higher AS (estimate ± 1 SE: 93.36 ± 43.26, $t_{13} = 2.16$, $p = 0.050$; Figure 4C) compared with parr that were maintained in the OM treatment throughout the experiment.

Parr initially maintained in the sand treatment and moved in the parr stage to the gravel treatment (S–G) had a marginally significantly lower AS (estimate ± 1 SE: −75.73 ± 40.05, $t_{15} = -1.89$, $p = 0.078$; Figure 4C) compared with parr remaining in the gravel treatment (G–G). They also had a tendency for a lower mass (estimate ± 1 SE: −375.89 ± 191.28, $t_{18} = -1.95$, $p = 0.065$; Figure 5A), but no other significant differences were observed.

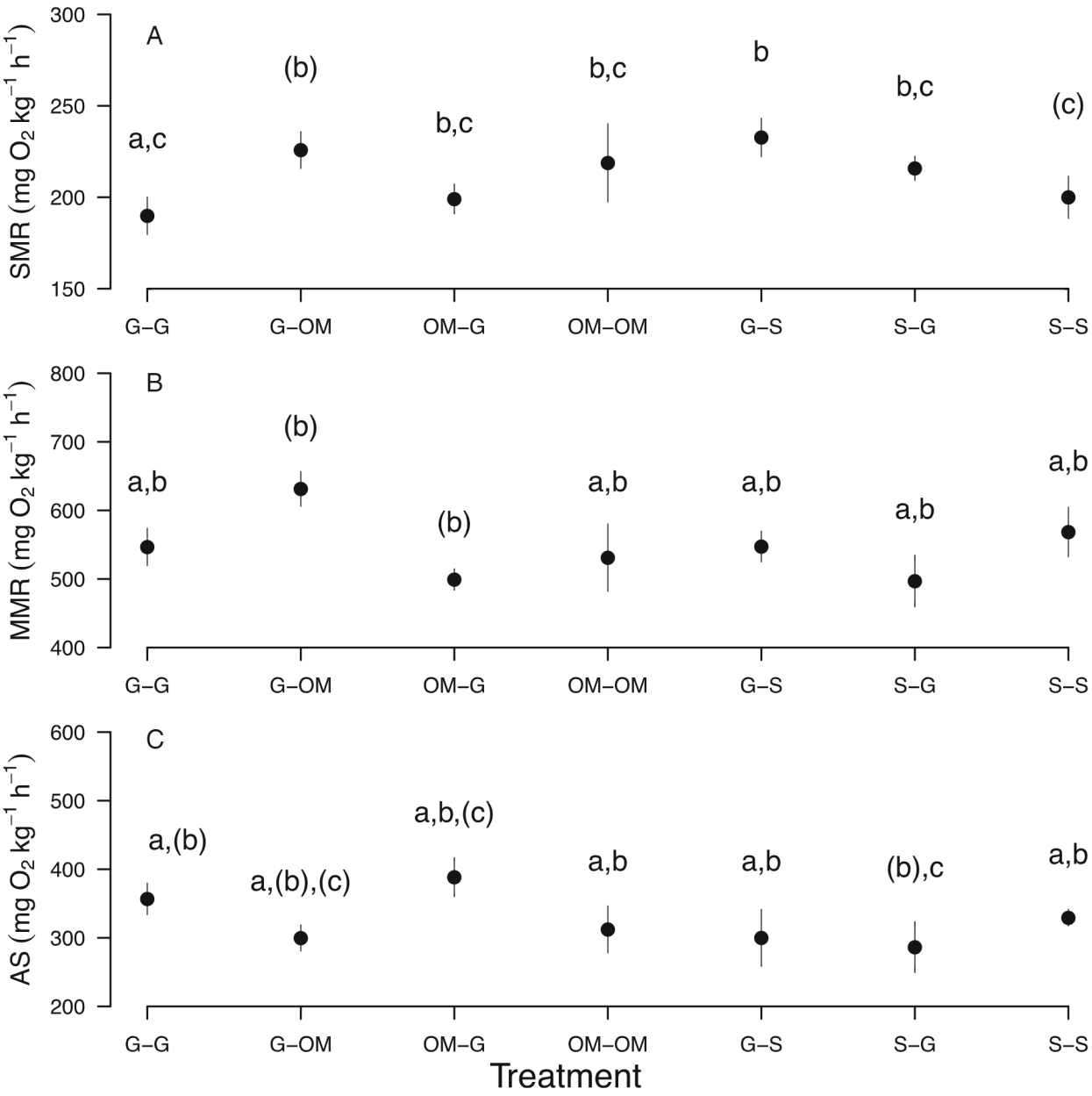


**FIGURE 4** Mean (±1 SE) standard metabolic rate (SMR) (A), maximum metabolic rate (MMR) (B), and aerobic scope (AS) (C) in the seven treatments in Phase 2 of the experiment (G–G: gravel–gravel, G–OM: gravel–organic matter, G–S: gravel–sand, OM–OM: organic matter–organic matter, OM–G: organic matter–gravel, S–S: sand–sand, S–G: sand–gravel). Treatments not sharing the same letter differ significantly ($p < 0.05$), and a difference was detected at the 0.07 level when letters are in parentheses. Note the differences in the vertical axis between subfigures.

## DISCUSSION

### Phase 1: Carryover effects expressed from eggs to fry

Studies on the differential success of individuals in critical life-history stages can promote the understanding of the ways in which populations respond to the carryover effects of changing environmental conditions. Here, organic matter and sand were found to have significant but differing effects on several variables measured in the early stages of brown trout. The survival of eggs was lower in both sand and OM treatments compared with the gravel treatment with no added sediment, and similarly to Del Rio et al. (2021), RMR was also significantly lower in OM. In salmonids, oxygen is supplied to the embryo by water flowing past the eggs through their boundary layer, and it is highly influenced by the

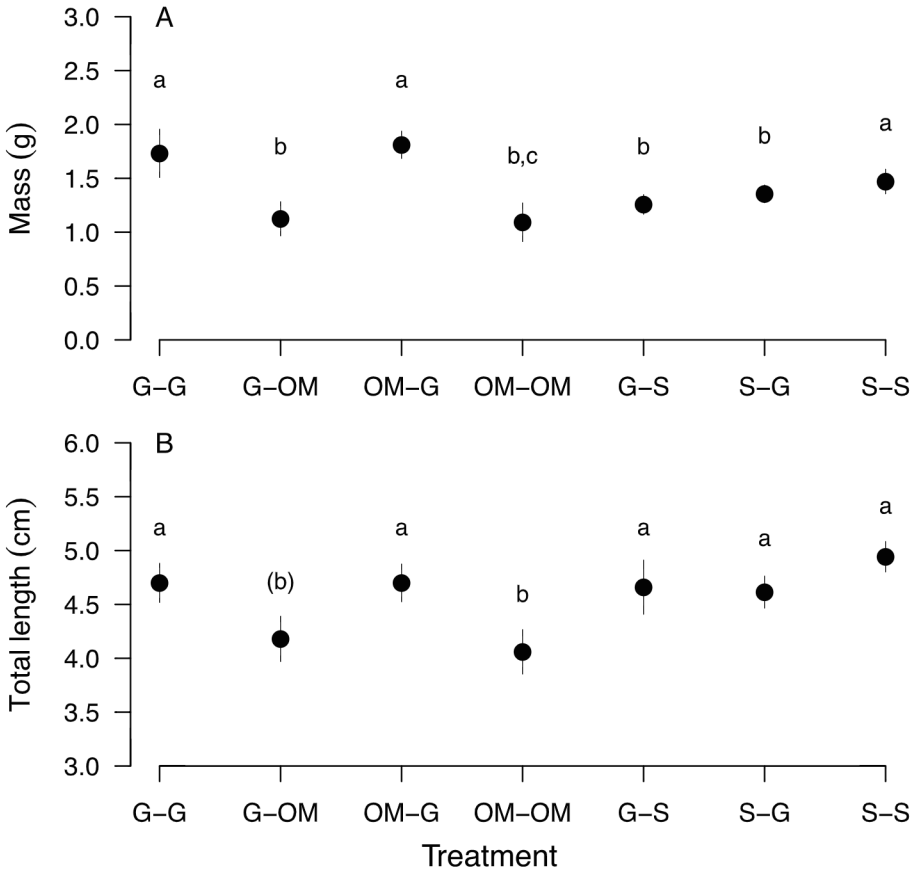


**FIGURE 5** Mean (±1 SE) mass (A) and total length (B) in the seven treatments in Phase 2 of the experiment. Abbreviations are as in Figure 4. Treatments not sharing the same letter differ significantly ($p < 0.05$), and a difference was detected at the 0.07 level when letters are in parentheses.

interstitial velocity and fine sediment concentration (Malcolm et al., 2008). Very fine sediment may be particularly harmful for developing embryos, as it is physically able to block the micropore canals in the egg membrane (Greig et al., 2005), whereas silt or fine sand reduces permeability and the intragravel flow necessary for the oxygenation of eggs within spawning beds (Levasseur et al., 2006). OM entering substrate interstices depletes oxygen and reduces dissolved oxygen concentrations, and it prevents a sufficient exchange of necessary gases from water flow to eggs, and vice versa (Bilotta & Braziera, 2008).

Indeed, there is no doubt that a decline in the productivity of spawning habitats is linked to the intrusion and accumulation of fine sediment into salmonid redds (Sear et al., 2017), but the causal pathways of nonlethal processes are still undetermined. In this study, organic matter had multiple nonlinear relationships with the size and metabolic measurements of emerged fry, and these are likely to have an impact on growth, competitive ability, and the further performance of juveniles. Accordingly, organic matter has been identified as among the major causes of reduced development of salmonid eggs, especially in "peatland-rich" countries. In the Baltic Sea drainage basin, for example, a total of 10 Mha of 19.5 Mha of existing mires (i.e., peatlands) have been drained to improve forest growth (Finér et al., 2021). This drainage has been particularly intensive in Finland, where 4.7 Mha of peatlands and 1.3 Mha of mineral soil sites have been drained, mostly in the 1960s–1970s (Vaahtera et al., 2018). Thus, waters enriched in organic matter are widespread (Nieminen et al., 2021), and declining water quality is a serious threat to the survival of several fish species, and even to the success of restoration efforts (Marttila et al., 2019; Syrjänen et al., 2017). The results here reveal complex relationships with the detrimental carryover effects of organic matter, but better understanding of the causal links requires both laboratory experiments and field studies in the future (Álvarez & Nicieza, 2005).

Body size is considered as one of the most important factors affecting the survival of early juveniles, and variation in early stages has profound effects on fish in adulthood and their later fitness (Miller et al., 1988). For example, the age at smoltification, maturation, and

overall growth rates of Atlantic salmon are determined by body size and lipid reserves over the first periods of life (Thorpe et al., 1998). However, alevins maintained in the OM treatment were not only longer but also had a larger yolk sac than that of gravel- and sand-treated conspecifics, which was contradictory to our expectations. Although this could be partly attributed to difficulties in sampling, it appears likely that some of the yolk reserves were not allocated to growth, probably revealing a physiological stress response (Valdimarsson et al., 2002). Similar conflicting findings have also been reported by Alberto et al. (2017). The reduced RMR in the OM treatment at the egg stage could possibly also explain why fish in next life stage had more energy reserves left. The greater length of alevins in the OM treatment was not, however, persistent, as these fish were significantly smaller in the parr stage (OM–OM) than those that spent all of their early life in the gravel treatment (G–G). Typically, however, growth rates are reduced when the yolk conversion efficiency is lower (Kamler, 2008). Indeed, emerging individuals should maximize their body size given the available amount of yolk reserves, as large individuals are also generally less vulnerable to size-selective predation (Anderson, 1988) and have better competitiveness. In addition, if juveniles do not have sufficient swimming ability, they will be vulnerable to downstream displacement by water flow during the first couple of weeks (Heggenes & Traaen, 1988).

Interestingly, the differences in size parameters and energy stores were no longer apparent by the time of emergence, and the only clear difference was noticed in the duration of the emergence period. As the period of emergence was clearly longest in the sand treatment, fine sand may alter or disrupt the emergence period. We suggest that this supports the *ready-or-not* hypothesis modified by Bailey et al. (2010) from the *match–mismatch* hypothesis (Frank & Leggett, 1994). The original hypothesis emphasized an optimal seasonal window within which individuals should undergo their key life-cycle events to succeed in their performance, and *ready-or-not* reinforces the original hypothesis by also recognizing the developmental "readiness" of fish, which may influence their performance and fitness under prevailing environmental conditions. In their experiment, Bailey et al. (2010) found larger and more advanced hatchery-reared fry to benefit from their later emergence when released into the wild as compared with earlier emergence as less developed fry. As natural populations could be expected to be adapted to the natural environment both ontogenetically (i.e., terms of developmental condition) and phenologically (i.e., in terms of optimal timing), this asynchrony in timing and development was suggested to provide evidence of stabilizing selection and thereby to complement the *ready-or-not* hypothesis. Although their experiment was more focused on assessing the strength and pattern of selection acting on captive-bred salmon released into the wild, we argue that habitat quality during embryogenesis has carryover effects on the developmental readiness of emerging fry and thereby on their further performance, as also reported by Einum and Fleming (2000).

Escape responses involving fast start swimming allow fish to avoid sudden dangers or optimize feeding in their environment. As these fast starts are fuelled anaerobically, adaptations for good fast start performance are thought to include a large proportion of white muscle relative to red (Webb, 1984) and for this proportion to reach its maximum just as brown trout fry begin to search for external food (Hale, 1999). Even if some of the fry in our experiment managed to survive over the long winter months in our experiment, their nonlocomotor variables were damped or delayed by sand, probably via effects on the development of sensory performance under hypoxic conditions. Similarly, previous studies have demonstrated that exposure to acute hypoxia reduces the responsiveness of seabass and gray mullet (*Liza aurata*) to a similar stimulus, but not the latency time (Lefrançois & Domenici, 2006). Overall, this nonlethal consequence of fine sand is likely to reduce the overall survival or fitness of juveniles if they were to establish their territories as their wild counter specifics. As the addition of sand forced fish to unsustainably use anaerobic metabolism (discussed more later) either by reducing the oxygen content of gravel interstices or delaying the emergence of fry, they would more likely to be caught by predators or displaced in the natural environment than juveniles with prompt reactions.

## Phase 2: Carryover effects expressed from fry to parr

In Phase 2, the gravel-treated fry were significantly smaller and they had a higher metabolic rate when they were placed in either the OM or sand treatment as parr. This phenotypic plasticity was not as evident when the treatments were reversed, that is, when eggs incubated in the OM treatment were moved to the gravel treatment in the parr stage. Instead, these juveniles were larger, and the pattern was only observed following transfer from sand to gravel treatments. Fish that have experienced unusually harsh periods, such as a low temperature or shortage of food, have been reported to compensate for the lost energy reserves later (Morgan & Metcalfe, 2001), but this was only slightly supported by our findings. Thus, it is reasonable to suggest that not only the incubation period but also the first 5–6 weeks after emergence are critical for recruitment to the population, and the

plasticity occurring during this period is not necessarily always adaptive.

To our knowledge, this is the first time that the metabolism of juvenile fish has been linked to the habitat conditions experienced in early life stages. Previous studies have exposed salmonid eggs to different oxygen contents and varying temperatures in the laboratory (e.g., Cook et al., 2018; Durtsche et al., 2021), but the links between changing habitat conditions and metabolism have not previously been quantified. SMR is the minimum metabolic rate to sustain life, while MMR represents the maximum energy production capacity of fish, and their difference, AS, defines the energy available, for example, for growth, feeding, and predator avoidance. The overall finding that parr moved to a less suitable habitat after incubation in a better environment were smaller but had a higher SMR highlights the importance of carryover effects of environmental conditions, even during the first weeks of survival in open water. The high SMR was most likely due to stress caused by the change in habitat quality, which means that fish have a higher cost of living and less available energy, for instance, for growth and swimming, as their growth tended to be reduced even though AS did not significantly change. Smaller fish have a lower probability of outcompeting individuals of their own species and thereby gaining preferential access to food through their higher status in the social hierarchy (Metcalfe et al., 1995), although contradictory results have also been reported (Norin & Malte, 2011).

To conclude, our findings highlight the need for future research in the context of multiple stressors and attempts to conserve threatened populations. Carryover effects can be persistent, occurring during exposure to a stressor and remaining present over the critical life shift until the stressor is removed, or they can be latent, where the effects of exposure only appear in later life stages after the stressor is removed (Pechenik, 2006). The current research lends support to both types of effects, as early exposure of eggs induced changes that were persistent until later life stages. However, the measured traits (growth and metabolism) were also plastic when fish were exposed to a new challenge as parr. Our study on the carryover effects of sedimentation on the early life stages of brown trout also has direct implications for fish management and for habitat restoration in particular. Salmonid fish in currently fast-changing environments are often forced to use suboptimal habitats, which may be subjected to sediment and other stressors, and improving the riverine habitats has become one of the main strategies to maintain self-sustaining populations of economically valuable fish populations in the face of human impacts.

Although restoration projects over the past decades have mostly been able to increase the abundance of salmonids, the sound geomorphic foundation of restoration schemes has also been proclaimed in the scientific community (last reviewed in Foote et al., 2020). Our findings here highlight the need to more widely improve habitats for juveniles searching for and establishing their territories, and the need to treat complete watersheds in restoration schemes instead of random and loosely connected in-stream sections of rivers or streams. Attempts to increase fish abundance without identifying potential limitations resulting from land use changes, such as sediment or nutrient loading in peatland-rich areas or insufficient hydrological connections within the entire watershed, are likely to be ineffective, particularly as climate warming progresses. When the scope of restoration projects is too narrow, the results may initially appear promising, but later during the parr stage, fish populations may suffer from the carryover effects of exposure to environmental stressors or experience density-dependent mortality (Einum et al., 2008), and there is no lasting influence on the overall life cycle. Thus, ensuring sufficient spatial dispersion to suitable habitats for organisms and considering their ontogenetic niche shifts with differing habitat requirements, together with sufficient water protection methods, would have better lasting effects and support management strategies.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Louhi et al., 2022) are available from Zenodo: https://doi.org/10.5281/zenodo.6984676.

## REFERENCES

Alberto, A., S. C. Courtenay, A. St-Hilaire, and M. R. van den Heuvel. 2017. "Factors Influencing Brook Trout (*Salvelinus fontinalis*) Egg Survival and Development in Streams Influenced by Agriculture." *Journal of FisheriesSciences.com* 11: 9–20.

Allan, I. R. H., and J. A. Ritter. 1977. "Salmonid Terminology." *ICES Journal of Marine Science* 37: 293–9.

Álvarez, D., and A. G. Nicieza. 2005. "Is Metabolic Rate a Reliable Predictor of Growth and Survival of Brown Trout (*Salmo trutta*) in the Wild?" *Canadian Journal of Fisheries and Aquatic Sciences* 62: 643–9.

Anderson, J. T. 1988. "A Review of Size Dependent Survival during Pre-Recruit Stages of Fishes in Relation to Recruitment." *Journal of Northwest Atlantic Fishery Science* 8: 55–66.

Anttila, K., M. Lewis, J. M. Prokkola, M. Kanerva, E. Seppänen, I. Kolari, and M. Nikinmaa. 2015. "Warm Acclimation and Oxygen Depletion Induce Species-Specific Responses in Salmonids." *Journal of Experimental Biology* 218: 1471–7.

Bailey, M. M., K. A. Lachapelle, and M. T. Kinnison. 2010. "Ontogenetic Selection on Hatchery Salmon in the Wild: Natural Selection on Artificial Phenotypes." *Evolutionary Applications* 3: 340–51.

Bilotta, G. S., and R. E. Braziera. 2008. "Understanding the Influence of Suspended Solids on Water Quality and Aquatic Biota." *Water Research* 42: 2849–61.

Bloomer, J., D. Sear, and P. Kemp. 2018. "Does Variation in Egg Structure among Five Populations of Atlantic Salmon (*Salmo salar*) Influence Their Survival in Low Oxygen Conditions?" *Royal Society Open Science* 6: 181020.

Brown, W. C., and R. Hanson. 2020. "Computer Program Tracker Video Analysis and Modeling JS (Beta)." Version 5.9, WWW Document. https://tracker.physlets.org/trackerJS/.

Cadiz, L., B. Ernande, P. Quazuguel, A. Servili, J.-L. Zambonino-Infante, and D. Mazurais. 2018. "Moderate Hypoxia but Not Warming Conditions at Larval Stage Induces Adverse Carry-Over Effects on Hypoxia Tolerance of European Sea Bass (*Dicentrarchus labrax*) Juveniles." *Marine Environmental Research* 138: 28–35.

Cadiz, L., J.-L. Zambonino-Infante, P. Quazuguel, L. Madec, H. Le Delliou, and D. Mazurais. 2018. "Metabolic Response to Hypoxia in European Sea Bass (*Dicentrarchus labrax*) Displays Developmental Plasticity." *Comparative Biochemistry and Physiology, Part B* 215: 1–9.

Chabot, D., J. F. Steffensen, and A. P. Farrell. 2016. "The Determination of Standard Metabolic Rate in Fishes." *Journal of Fish Biology* 88: 81–121.

Cook, C. J., C. C. Wilson, and G. Burness. 2018. "Impacts of Environmental Matching on the Routine Metabolic Rate and Mass of Native and Mixed-Ancestry Brook Trout (*Salvelinus fontinalis*) Fry." *Conservation Physiology* 6: coy023.

Del Rio, A. M., G. N. Mukai, B. T. Martin, R. C. Johnson, N. A. Fangue, J. A. Israel, and A. E. Todgham. 2021. "Differential Sensitivity to Warming and Hypoxia during Development and Long-Term Effects of Developmental Exposure in Early Life Stage Chinook Salmon." *Conservation Physiology* 9: coab054.

Domenici, P., B. J. M. Allan, C. Lefrançois, and M. I. McCormick. 2019. "The Effect of Climate Change on the Escape Kinematics and Performance of Fishes: Implications for Future Predator–Prey Interactions." *Conservation Physiology* 7: coz078.

Domenici, P., and R. W. Blake. 1997. "The Kinematics and Performance of Fish Fast-Start Swimming." *Journal of Experimental Biology* 200: 1165–78.

Durtsche, D. R., B. Jonsson, and L. Greenberg. 2021. "Thermal Conditions during Embryogenesis Influence Metabolic Rates of Juvenile Brown Trout *Salmo trutta*." *Ecosphere* 12: e03374.

Einum, S., and I. A. Fleming. 2000. "Selection against Late Emergence and Small Offspring in Atlantic Salmon (*Salmo salar*)." *Evolution* 54: 628–39.

Einum, S., K. H. Nislow, J. D. Reynolds, and W. J. Sutherland. 2008. "Predicting Population Responses to Restoration of Breeding Habitat in Atlantic Salmon." *Journal of Animal Ecology* 45: 930–8.

Elliott, J. M. 1994. *Quantitative Ecology and the Brown Trout. Oxford Series in Ecology and Evolution*. Oxford: Oxford University Press. 298 pp.

Finér, L., A. Lepistö, K. Karlsson, A. Räike, L. Härkönen, M. Huttunen, S. Joensuu, et al. 2021. "Drainage for Forestry Increases N, P and TOC Export to Boreal Surface Waters." *Science of the Total Environment* 762: 144098.

Finstad, A. G., S. Einum, T. Forseth, and O. Ugedal. 2007. "Shelter Availability Affects Behaviour, Size-Dependent and Mean Growth of Juvenile Atlantic Salmon." *Freshwater Biology* 52: 1710–8.

Foote, K. J., P. M. Biron, and J. W. A. Grant. 2020. "Impact of In-Stream Restoration Structures on Salmonid Abundance and Biomass: An Updated Meta-Analysis." *Canadian Journal of Fisheries and Aquatic Sciences* 77: 1574–91.

Frank, K. T., and W. C. Leggett. 1994. "Fisheries Ecology in the Context of Ecological and Evolutionary Theory." *Annual Review of Ecology and Systematics* 25: 401–22.

Fuiman, L. A., K. A. Rose, J. H. Cowan, and E. P. Smith. 2006. "Survival Skills Required for Predator Evasion by Fish Larvae and Their Relation to Laboratory Measures of Performance." *Animal Behaviour* 71: 1389–99.

Greig, S. M., D. A. Sear, and P. A. Carling. 2005. "The Impact of Fine Sediment Accumulation on the Survival of Incubating Salmon Progeny: Implications for Sediment Management." *Science of the Total Environment* 344: 241–58.

Hale, M. E. 1999. "Locomotor Mechanics during Early Life History: Effects of Size and Ontogeny on Fast-Start Performance of Salmonid Fishes." *Journal of Experimental Biology* 202: 1465–79.

Heggenes, J., and T. Traaen. 1988. "Downstream Migration and Critical Water Velocities in Stream Channels for Fry of Four Salmonid Species." *Journal of Fish Biology* 32: 717–27.

Hertta 5.7. Open Data Source. 2019. "Finnish Environment Institute and Regional Ely-Centers." https://www.syke.fi/fi-FI/Avoin_tieto/Ymparistotietojarjestelmat.

IPCC. 2021. "Summary for Policymakers." In *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, et al., 3–31. Cambridge: Cambridge University Press. https://doi.org/10.1017/9781009157896.

Johnston, E. F., S. L. Alderman, and T. E. Gillis. 2013. "Chronic Hypoxia Exposure of Trout Embryos Alters Swimming Performance and Cardiac Gene Expression in Larvae." *Physiological and Biochemical Zoology* 86: 567–75.

Jones, M., A. Laurila, N. Peuhkuri, J. Piironen, and T. Seppä. 2003. "Timing an Ontogenetic Niche Shift: Responses of Emerging

Salmon Alevins to Chemical Cues from Predators and Competitors." *Oikos* 102: 155–63.

Jonsson, B., and L. Greenberg. 2021. "Egg Incubation Temperature Influences the Population-Specific Outmigration Rate of Juvenile Brown Trout *Salmo trutta*." *Journal of Fish Biology* 100: 909–17.

Jonsson, B., and N. Jonsson. 2019. "Phenotypic Plasticity and Epigenetics of Fish: Embryo Temperature Affects Later-Developing Life-History Traits." *Aquatic Biology* 28: 21–32.

Jonsson, B., N. Jonsson, and M. M. Hansen. 2022. "Knock-On Effects of Environmental Influences during Embryonic Development of Ectothermic Vertebrates." *The Quarterly Review of Biology* 97: 95–139.

Kamler, E. 2008. "Resource Allocation in Yolk-Feeding Fish." *Reviews in Fish Biology and Fisheries* 18: 143–200.

Kemp, P., D. Sear, A. Collins, P. Naden, and I. Jones. 2011. "The Impacts of Fine Sediment on Riverine Fish." *Hydrological Processes* 25: 1800–21.

Lefrançois, C., and P. Domenici. 2006. "Locomotor Kinematics and Behaviour in the Escape Response of European Sea Bass, *Dicentrarchus labrax* L., Exposed to Hypoxia." *Marine Biology* 149: 969–77.

Levasseur, M., N. E. Bergeron, M. F. Lapointe, and F. Bérubé. 2006. "Effects of Silt and Very Fine Sand Dynamics in Atlantic Salmon (*Salmo salar*) Redds on Embryo Hatching Success." *Canadian Journal of Fisheries and Aquatic Sciences* 63: 1450–9.

Louhi, P., A. Mäki-Petäys, J. Erkinaro, A. Paasivaara, and T. Muotka. 2010. "Impacts of Forest Drainage Improvement on Stream Biota: A Multisite BACI-Experiment." *Forest Ecology and Management* 260: 1315–23.

Louhi, P., M. Ovaska, A. Mäki-Petäys, J. Erkinaro, and T. Muotka. 2011. "Does Fine Sediment Constrain Salmonid Alevin Development and Survival?" *Canadian Journal of Fisheries and Aquatic Sciences* 68: 1819–26.

Louhi, P., L. Pettinau, L. S. Härkönen, K. Anttila, and A. Huusko. 2022. "Data From: Carry-Over Effects of Environmental Stressors Influence the Life Performance of Brown Trout." Data Set. Zenodo. https://doi.org/10.5281/zenodo.6984676.

Malcolm, I. A., A. F. Youngson, S. Greig, and C. Soulsby. 2008. "Hyporheic Influences on Spawning Success." In *Salmon Spawning Habitat in Rivers: Physical Controls, Biological Responses and Approaches to Remediation*, edited by D. Sear and P. DeVries, 225–48. Bethesda, MD: American Fisheries Society.

Marras, S., S. S. Killen, G. Claireaux, P. Domenici, and D. J. McKenzie. 2011. "Behavioural and Kinematic Components of the Fast-Start Escape Response in Fish: Individual Variation and Temporal Repeatability." *Journal of Experimental Biology* 214: 3102–10.

Marttila, M., P. Louhi, A. Huusko, T. Vehanen, A. Mäki-Petäys, J. Erkinaro, J. Syrjänen, and T. Muotka. 2019. "Synthesis of Habitat Restoration Impacts on Young-of-the Year Salmonids in Boreal Rivers." *Reviews in Fish Biology and Fisheries* 29: 513–27.

Metcalfe, N. B., A. C. Taylor, and J. E. Thorpe. 1995. "Metabolic Rate, Social Status and Life-History Strategies in Atlantic Salmon." *Animal Behaviour* 49: 431–6.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. "Larval Size and Recruitment Mechanisms in Fishes: Toward a Conceptual Framework." *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1657–70.

Morgan, I. J., and N. B. Metcalfe. 2001. "The Influence of Energetic Requirements on the Preferred Temperature of Overwintering Juvenile Atlantic Salmon (*Salmo salar*)." *Canadian Journal of Fisheries and Aquatic Sciences* 58: 762–8.

Murdoch, A., C. Mantyka-Pringle, and S. Sharma. 2020. "The Interactive Effects of Climate Change and Land Use on Boreal Stream Fish Communities." *Science of the Total Environment* 700: 134518.

Newcombe, C. P., and O. T. Jensen. 1996. "Channel Suspended Sediment and Fisheries: A Synthesis for Quantitative Assessment of Risk and Impact." *North American Journal of Fisheries Management* 16: 693–727.

Nieminen, M., S. Sarkkola, T. Sallantaus, E. M. Hasselquist, and H. Laudon. 2021. "Peatland Drainage—A Missing Link behind Increasing TOC Concentrations in Waters from High Latitude Forest Catchments?" *Science of the Total Environment* 774: 145150.

Norin, T., and H. Malte. 2011. "Repeatability of Standard Metabolic Rate, Active Metabolic Rate and Aerobic Scope in Young Brown Trout during a Period of Moderate Food Availability." *Journal of Experimental Biology* 214: 1668–75.

O'Connor, C. M., D. R. Norris, G. T. Crossin, and S. J. Cooke. 2014. "Biological Carryover Effects: Linking Common Concepts and Mechanisms in Ecology and Evolution." *Ecosphere* 5: 28.

Ostrovsky, I. 1995. "The Parabolic Pattern of Animal Growth: Determination of Equation Parameters and Their Temperature Dependencies." *Freshwater Biology* 33: 357–71.

Pechenik, J. A. 2006. "Larval Experience and Latent Effects—Metamorphosis Is Not a New Beginning." *Integrative and Comparative Biology* 46: 323–33.

Piggott, J. J., C. R. Townsend, and C. D. Matthaei. 2015. "Reconceptualizing Synergism and Antagonism among Multiple Stressors." *Ecology and Evolution* 5: 1538–47.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and The R Development Core Team. 2017. "nlme: Linear and Nonlinear Mixed Effects Models." R Package Version 3.1-131. http://www.r-project.org/package=nmle.

Pont, D., B. Hugueny, U. Beier, D. Goffaux, A. Melcher, R. Noble, C. Rogers, N. Roset, and S. Schmutz. 2006. "Assessing River Biotic Condition at a Continental Scale: A European Approach Using Functional Metrics and Fish Assemblages." *Journal of Applied Ecology* 43: 70–80.

Rasband, W. S. 2018. *ImageJ*. Bethesda, MD: U. S. National Institutes of Health. https://imagej.nih.gov/ij/.

Roussel, J.-M. 2007. "Carry-Over Effects in Brown Trout (*Salmo trutta*): Hypoxia on Embryos Impairs Predator Avoidance by Alevins in Experimental Channels." *Canadian Journal of Fisheries and Aquatic Sciences* 64: 786–92.

Schindelin, J., I. Arganda-Carreras, E. Frise, V. Kaynig, M. Longair, T. Pietzsch, S. Preibisch, et al. 2012. "Fiji: An Open-Source Platform for Biological-Image Analysis." *Nature Methods* 9: 676–82.

Sear, D. A., I. Pattison, A. L. Collins, D. J. Smallman, J. I. Jones, and P. S. Naden. 2017. "The Magnitude and Significance of Sediment Oxygen Demand in Gravel Spawning Beds for the Incubation of Salmonid Embryos." *River Research and Applications* 33: 1642–54.

Skoglund, H., S. Einum, and G. Robertsen. 2011. "Competitive Interactions Shape Offspring Performance in Relation to Seasonal Timing of Emergence in Atlantic Salmon." *Journal of Animal Ecology* 80: 365–74.

Smialek, N., J. Pander, and J. Geist. 2021. "Environmental Threats and Conservation Implications for Atlantic Salmon and Brown Trout during Their Critical Freshwater Phases of Spawning, Egg Development and Juvenile Emergence." *Fisheries Management and Ecology* 28: 437–67.

Sullivan, S. M. P., and M. C. Watzin. 2010. "Towards a Functional Understanding of the Effects of Sediment Aggradation on Stream Fish Condition." *River Research and Applications* 26: 1298–310.

Svendsen, M. B. S., P. G. Bushnell, and J. F. Steffensen. 2016. "Design and Setup of Intermittent Flow Respirometry System for Aquatic Organisms." *Journal of Fish Biology* 88: 26–50.

Svendsen, M. B. S., P. G. Bushnell, and J. F. Steffensen. 2019. "AquaResp 3." Zenodo. https://doi.org/10.5281/zenodo.2584015.

Syrjänen, J. T., A. Vainikka, P. Louhi, A. Huusko, P. Orell, and T. Vehanen. 2017. "History, Conservation and Management of Adfluvial Brown Trout Stocks in Finland." In *Brown Trout: Biology, Ecology and Management*, edited by J. Lobòn-Cerviá and N. Sanz, 697–734. Chichester: John Wiley & Sons.

Thorpe, J. E., M. Mangel, N. B. Metcalfe, and F. A. Huntingford. 1998. "Modelling the Proximate Basis of Salmonid Life-History Variation, with Application to Atlantic Salmon, *Salmo salar* L." *Evolutionary Ecology* 12: 581–99.

Vaahtera, E., M. Aarne, A. Ihalainen, E. Mäki-Simola, A. Peltola, J. Torvelainen, E. Uotila, and E. Ylitalo, eds. 2018. *Finnish Forest Statistics*. Helsinki: Luonnonvarakeskus. 188 pp.

Valdimarsson, K., S. Skularon, and S. Snorrason. 2002. "The Relationship between Egg Size and the Rate of Early Development in Arctic charr, *Salvelinus alpinus*." *Environmental Biology of Fishes* 65: 463–8.

Webb, P. W. 1984. "Body Form, Locomotion and Foraging in Aquatic Vertebrates." *American Zoologist* 24: 107–20.

Welcomme, R. L., K. O. Winemiller, and I. G. Cowx. 2006. "Fish Environmental Guilds as a Tool for Assessment of Ecological Condition of Rivers." *River Research and Applications* 22: 377–96.

Wood, S. 2021. "Package 'mgcv' Mixed GAM Computation Vehicle with Automatic Smoothness Estimation." Version 1.8-38. https://cran.r-project.org/web/packages/mgcv/mgcv.pdf.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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