

# A permeable hyporheic zone may contribute to buffer the effects of a drying event on prey availability for salmonid juveniles

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**Abstract** – Climate change is increasing the intensity and frequency of hydrological events in freshwater. Summer droughts and drying events drastically reduce the favourable habitat for aquatic organisms shaping interactions among species. Macroinvertebrates are usually less abundant during severe summer low flows, reducing prey availability for carnivorous fish, such as brown trout (*Salmo trutta*). To quantify the consequences of a surface water drying event on fish performance, we conducted an experiment in 6 experimental channels naturally fed by water and macroinvertebrates. After a colonisation period for macroinvertebrates, the water level was dropped to the benthic surface for two weeks in 3 channels, while it remained constant in the 3 other channels. After water level restoration, juvenile brown trout were reared for three weeks in the control and dry channels. The drying event did not reduce the abundance of macroinvertebrates. Survival and growth of juvenile trout were unaffected by drying. Our experiment provided circumstantial evidence that the hyporheic zone could potentially serve as an effective refuge for macroinvertebrates, mitigating the effects of drying events on food webs, although this mitigation would strongly depend on sediment characteristics, habitat quality and the composition of the macroinvertebrate community.

**Keywords:** Drying event / young-of-the-year / survival / growth / macroinvertebrates

## 1 Introduction

Pickett and White (1985) defined natural disturbance as a relatively discrete event in time that disrupts ecosystems, including communities, as well as changing the physical environment. In natural ecosystems, communities are subject to disturbances of different frequencies and intensities (Downes *et al.*, 1998). Organisms may adapt to predictable seasonal fluctuations (photoperiod, discharge, temperature, *etc.*), but adapt with difficulty to disturbances that vary greatly in their frequency and intensity over temporal and spatial scales (Resh *et al.*, 1988). In rivers, hydrological disturbances are major sources of mortality both for macroinvertebrates and fish (Naiman *et al.*, 2008). With climate change, summer droughts and drying events are expected to become increasingly severe and prolonged in European rivers (Trenberth *et al.*, 2014; Dayon *et al.*, 2018; Reid *et al.*, 2019) because of the predicted reduction of precipitation levels together with increased evapotranspiration as both air and

water temperatures rise. Additionally, water deficits are expected to be exacerbated by increased water uses for human activities (*i.e.*, agriculture, industry or drinking water, Palmer *et al.*, 2009).

In streams, climate is a strong driver for fish assemblages (Magalhães *et al.*, 2007), including for salmonid populations (Zabel *et al.*, 2006; Walsh and Kilsby, 2007), with severe consequences for development, growth, behaviour, survival and population dynamics (Clews *et al.*, 2010). During droughts and low flow periods, shallow sections (such as riffles and runs) disappear and streams become a series of fragmented pools (Lake, 2003). Fish emigration is prevented (Elliott *et al.*, 1997; Armstrong *et al.*, 2003) and fish are confined to restricted areas with a high risk of mortality from desiccation, predation, starvation or suboptimal environmental conditions, particularly regarding dissolved oxygen concentration (Magalhães *et al.*, 2002). For example, Elliott (2000) demonstrated that severe droughts affected the trout population of Black Brows Beck (UK) by increasing mortality and limiting the growth of both juveniles and adults, which was partly attributed to a decrease in resource availability.

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Although macroinvertebrate larvae can use the hyporheic zone as a refuge when facing drying events, their response is highly context dependent (Wood *et al.*, 2010). Several studies reported an increase in the abundance of macroinvertebrates in the hyporheic zone during adverse conditions in surface streams (e.g. floods or drying events), whilst others did not observe any significant changes in macroinvertebrate distribution (Dole-Olivier, 2011; Stubbington, 2012). Part of the reason for having these contradictory observations can be linked to macroinvertebrate taxa showing a very variable set of ecological traits (Fenoglio *et al.*, 2007). The assemblages of aquatic ecosystems regularly subjected to droughts are dominated by small or medium-sized, short-lived macroinvertebrates with aquatic respiration and aerial dispersal such as Chironomidae, Simuliidae and Ephemeroptera, which can very successfully use the hyporheic zone as refuge during streambed drying (Williams and Hynes, 1974; Boulton *et al.*, 1998). Additionally, the physico-chemical characteristics of the hyporheic zone of riffles could be more favourable to macroinvertebrate survival than the conditions in isolated pools created during droughts (e.g. cooler water temperatures, higher dissolved oxygen concentrations; Dewson *et al.*, 2007). Depending on the survival of macroinvertebrates during these hydrological events, the subsequent delivery rate of prey by drift to fish can highly change (Atkinson *et al.*, 2014; Chadd *et al.*, 2017). In this regard, Hakala and Hartman (2004) revealed that limited food availability caused by drought reduced body condition (body weight and fat reserves) and the winter survival of brook trout (*Salvelinus fontinalis*). The authors highlighted that a 10% decrease in adult weight caused by drought resulted in a reduction of young-of-the-year (YoY) production by 67% the following year. Thus, hydrological events can cause long-term effects and lead to the decline of fish populations.

In the present study, we tested the effect of a surface water drying event (with a continuous flow in the hyporheic zone) on the trophic availability of brown trout juveniles. In 6 experimental channels, a reference discharge was maintained for 48 days to allow macroinvertebrates to colonise. Then, the discharge was diminished by 80% and the water level was reduced to the benthic surface in 3 channels for 2 weeks. Hydraulic conditions in the 3 dry channels returned to reference conditions and juvenile brown trout were added in all 6 experimental channels during 3 weeks of growth. We hypothesized that macroinvertebrates use the hyporheic zone as a refuge, mitigating the decrease in macroinvertebrate abundance caused by the surface water drying event and, consequently, the negative impacts on the survival and growth of brown trout juveniles.

## 2 Materials and methods

### 2.1 Experimental design

This experiment was conducted at the National Institute of Agronomic and Environmental Research's (INRAE) experimental facilities authorised for animal experimentation (A640141). The experiment was carried out in strict accordance with the E.U. legal frameworks, specifically those relating to the protection of animals used for scientific purposes (*i.e.*, Directive 2010/63/EU), and under the French

legislation governing the ethical treatment of animals (Decret no. 2013-118, February 1<sup>st</sup>, 2013).

The experiment was conducted in 6 outdoor channels (L: 12 m, W: 52 cm and H: 25 cm), continuously fed by gravity with unfiltered water pumped from an outdoor reservoir (4500 m<sup>3</sup>), which gets water from the Aitzeguerria and the Lapitxuri brooks in south-western France (43°16' N, 1°28' W; Fig. 1). In each 12-metre-long channel, a layer of 10 cm of coarse substrate ( $\phi = 3$  cm) was uniformly distributed over the 10 central metres and kept in place by two 0.5 cm mesh grids on both sides. Seventeen cobbles ( $\phi = 7-8$  cm) per channel were added to provide shelter and visual isolation for fish. Channels were covered with a tarpaulin for the experiment to mimic brightness under the shade of trees in the Lapitxuri brook (684 lux on average, SD=418, Iso-tech digital light meter Lux-1335). Water temperature was recorded every hour using a temperature logger at each channel (mini logger IIT, Vemco; Fig. S1).

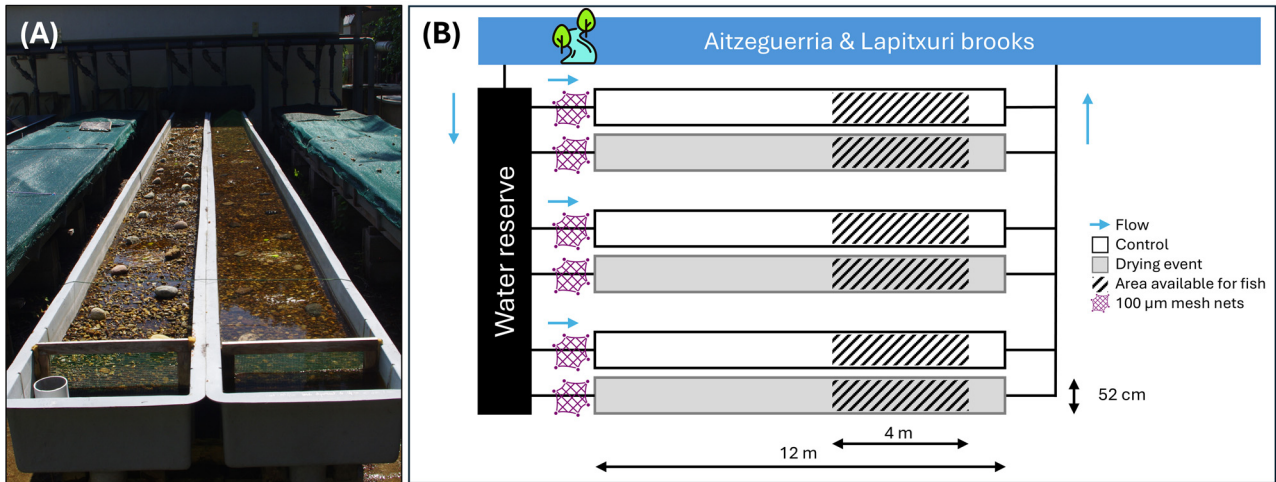
Before the start of the experiment (*i.e.*, from 12/05/2015 to 29/06/2015), the 6 channels received a discharge of 1 L s<sup>-1</sup> that created a water height of 4.5 cm above the substrate. These reference conditions were kept for 48 days to allow the natural colonisation of the channels by macroinvertebrates. After this colonisation period, a 100  $\mu$ m mesh net was placed in the water inlet of each channel to exclude the immigration of macroinvertebrates from the beginning of the drying event to the end of the experiment (Mureithi *et al.*, 2018; Slack *et al.*, 1991). The drying event was simulated in 3 channels and lasted two weeks. The discharge was reduced to 0.2 L s<sup>-1</sup> and the water height to 0 cm (benthic surface level). The other 3 channels were kept with the initial discharge. After the 2-week drying event, the 3 channels were brought back to reference discharge conditions.

### 2.2 Macroinvertebrates

Macroinvertebrates were sampled three times in the upstream, middle and downstream parts of each channel: before the drying event, after it and after the three weeks of fish rearing (see "Fish" section below). To obtain the macroinvertebrate samples, a corer with a 20 cm diameter was buried into the substrate, gravel was removed and macroinvertebrates in the water within the pipe pumped and sieved through a 500  $\mu$ m mesh and preserved in 70% ethanol. The locations for the first and second sampling corers were randomly chosen, but after the fish rearing period, two samples were collected in the 6-metre upstream channel section without trout and a sample in the 4-metre downstream section that had trout juveniles (see "Fish" section below). A total of fifty-four samples were obtained (three periods  $\times$  six channels  $\times$  three samples). Macroinvertebrates were identified and grouped into the following taxonomic groups: Diptera, Coleoptera, Oligochaeta, and "Others", which included all taxa representing less than 5% of total abundance (*i.e.*, Trichoptera, Ephemeroptera, Mollusca, Plecoptera and Crustacea).

### 2.3 Fish

Brown trout eggs were obtained through the artificial fertilization of gametes of wild brown trout (1♀  $\times$  1♂) caught in the Nivelle watershed and grew for 4 months under semi-natural conditions (artificial channel fed by a derivation from a



**Fig. 1.** Experimental design. Water levels were dropped onto the surface of the sediment in some channels (A, left channel), while 4.5 cm of water was maintained in others (A, right channel). (B) Channels were naturally fed by the Aitzeguerra and Lapitxuri brooks. After 48 days of colonisation by macroinvertebrates 100 µm mesh nets were placed at the beginning and end of the channels to study the dynamics of the community in place. A drying event was simulated for 15 days (grey channels) and then fish grew for 21 days (hatched areas).

headwater stream, the Lapitxuri brook, with natural food and substratum). A total of 102 juveniles were produced for the experiment. After a 24 h fasting period, juveniles were anesthetized (30 mg L<sup>-1</sup> benzocaine), individually weighed (wet mass) on a Sartorius CP153 electronic balance to the nearest 0.001 g, measured (total body length) to the nearest 1 mm and photographed for individual identification using melanophore distribution patterns (Garcia de Leaniz *et al.*, 1994). Trout were sorted into 6 similar batches (according to weight and length) of 17 fish with an average individual length of 55.67 mm (SD = 1.88) and an average individual mass of 8.76 g (SD = 1.00). Following recommendations by Grant and Kramer (1990), we estimated that the minimal area for the set of juveniles of this length (17 fish of 55 mm) was 2 m<sup>2</sup>. Thus, to rear fish under conditions close to habitat saturation, the downstream 4 m of the channels were separated from the top 6 meters by means of a 0.5 cm mesh grid (4 m long × 0.5 m wide = 2 m<sup>2</sup>), and fish were added only to this part of the channels. The top 6 meters had no fish but contributed to the production of drifting macroinvertebrates. After the drying event, fish were released into the 6 experimental channels for three weeks. They were recovered by electrofishing at the end and after a 24 h fasting period they were anesthetized, individually weighed, measured, and photographed. The performance of fish was estimated by means of survival rate, individual growth and condition factor. After the experiment, juveniles were released into the Lapitxuri brook.

## 2.4 Statistical analyses

Abundance of macroinvertebrates, survival, growth and condition factor of fish were analysed using a Bayesian modelling approach computed with OpenBUGS®.

### 2.4.1 Abundance of macroinvertebrates

Macroinvertebrates were sampled at 3 periods (*k*): before the drying event (*k*=1), after 2 weeks from the drying event (*k*=2) and after 3 weeks of trout growth (*k*=3). The abundance

of macroinvertebrates was therefore compared between control and dry channels for these 3 periods. We also evaluated the predation pressure exerted by the fish on macroinvertebrates by comparing the 6-meter upstream section (without trout) with the 4-meter downstream section of the channels (with trout). If *Abundance<sub>i</sub>* was the number of individuals counted in the *i*<sup>th</sup> sample, we assumed:

$$\mu \cdot \log(\text{Abundance}_i + 1)_i = \mu + \alpha_{k[i]} \text{Dry}_i + \beta_{j[i]} + \gamma_{k[i]} + \delta \text{Fish}_i$$

where  $\mu$  was the average of the logarithm for macroinvertebrate abundance,  $\alpha$  was a fixed-effect parameter for the differences between the control (Dry=0) and dry channels (Dry=1) before the drying event (*k*<sub>1</sub>), after 2 weeks of drying (*k*<sub>2</sub>) and after 3 weeks of trout growth (*k*<sub>3</sub>),  $\beta$  was a random effect corresponding to each *j* channel,  $\gamma$  was a random effect corresponding to the *k* steps and  $\delta$  was a fixed-effect parameter for trout predation pressure (*l*=0 without fish and *l*=1 with fish). The same modelling treatment was applied to the total abundance of the main macroinvertebrate groups (*i.e.*, Diptera, Coleoptera, Oligochaeta and "Others").

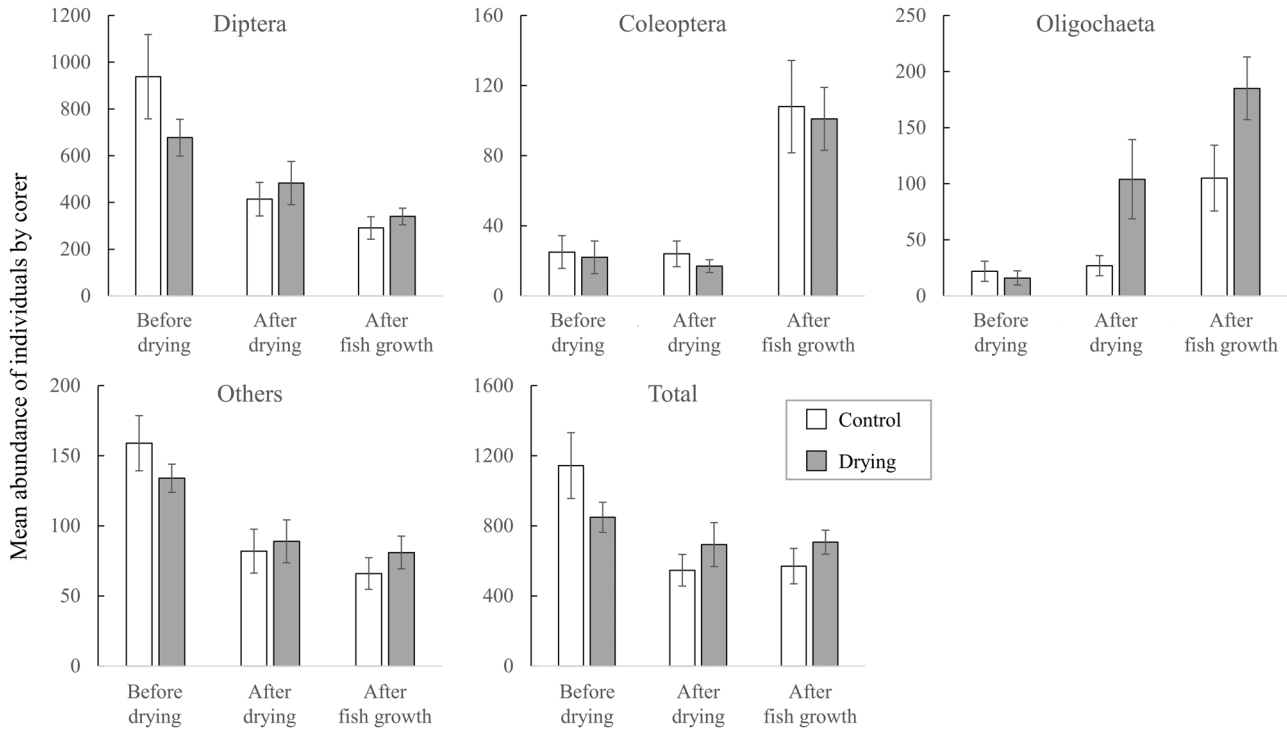
### 2.4.2 Survival of trout

Fish found outside the growing area or not recovered were not considered for the analyses (*S<sub>i</sub>*=0). Then, if *p.S<sub>i</sub>* was the probability of survival of the *i*<sup>th</sup> fish, we assumed:

$$S_i \sim \text{Bernoulli}(p.S_i)$$

$$\text{Logit}(p.S_i) = \mu + \alpha \text{Dry}_i + \beta_{j[i]}$$

where  $\mu$  was the mean of the logit for survival probability,  $\alpha$  was a fixed-effect parameter for the indirect impact of drying (Dry=0 for control and Dry=1 for dry channels) and  $\beta$  was a random effect corresponding to each *j* channel.



**Fig. 2.** Abundance of macroinvertebrates (mean number of individuals by corer) before the drying event, after 2 weeks of drying and after 3 weeks of fish growth in reference discharge conditions in the control and dry channels, shown in white and grey respectively. Each condition represents 9 samples, for a total of 54 samples. Error bars represent standard errors.

#### 2.4.3 Growth of trout

All the fish were weighed at the beginning of the growing period ( $W_{beg_i}$ ) and all the survivors were weighed at the end ( $W_{end_i}$ ). Photos allowed the individual recognition of juveniles and growth ( $G_i$ ) was calculated by dividing the difference between final and initial weight by initial weight (in g). We stated that the growth  $G_i$  followed normal distribution with  $\mu.G_i$  the mean and  $\sigma.G_i$  the standard deviation. We assumed:

$$\mu.G_i = \mu + \alpha Dry_i + \beta_{j[i]}$$

where  $\mu$  was the mean of the individual growth of juveniles,  $\alpha$  was a fixed-effect parameter for the indirect impact of drying (Dry=0 for control and Dry=1 for dry channels) and  $\beta$  was a random effect corresponding to each  $j$  channel.

#### 2.4.4 Condition factor of trout

Fulton's condition factor  $K$  for each  $i$  trout was calculated with empirical data by dividing the final weight (in mg) by length (in mm) cubed multiplied by 100 (Fulton, 1911). Then, we assumed:

$$\mu.K_i = \mu + \alpha Dry_i + \beta_{j[i]}$$

where  $\mu$  was the mean of the condition factor,  $\alpha$  was a fixed-effect parameter for the indirect impact of drying (Dry=0 for control and Dry=1 for the dry channels) and  $\beta$  was a random effect corresponding to each  $j$  channel.

#### 2.4.5 Bayesian computation

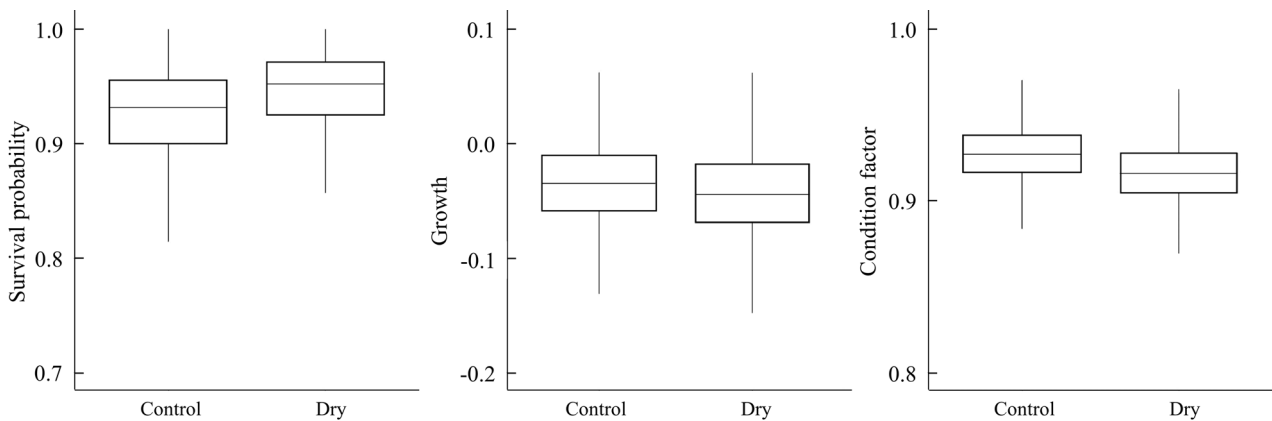
Parameters were given independent “weakly informative” priors (Tab. S1; Gelman, 2006; Gelman and Hill, 2007). For each analysis, three independent chains were used. The first 10,000 iterations were discarded as an initial burn-in period. Then, 10,000 further iterations (resulting from one every ten runs) were performed. The convergence of the chains to their ergodic distribution was tested *via* the Gelman-Rubin (GR) diagnostics integrated in OpenBUGS®. The significance of the parameters was tested by calculating the posterior probability of these parameters to be positive ( $P(X > 0) > 0.90$ ) or negative ( $P(X > 0) < 0.10$ ) (Gelman and Hill, 2007).

### 3 Results

The abundance of all macroinvertebrate groups was similar in the control and dry channels at all periods (before, after the drying event and after fish growth; Fig. 2, Tabs. 1, and S2), except for the abundance of Oligochaeta, which was significantly higher in the dry channels than in the control channels at the end of fish growth ( $\alpha_3 = 1.50$ ). The presence of fish significantly decreased the abundance of Diptera, Coleoptera and “Others” ( $\delta = -0.698$ ,  $-1.475$  and  $-0.826$ , respectively) as well as the total abundance ( $\delta = -0.717$ ) while it did not affect the abundance of Oligochaeta. Considering the periods, the abundance of different groups of macroinvertebrates shifted throughout the summer: the abundance of Coleoptera and Oligochaeta increased ( $\gamma_1 = \gamma_2$  and  $\gamma_2 < \gamma_3$ )

**Table 1.** Probability of a significant different abundance between control and dry channels ( $\alpha_1$ ,  $\alpha_2$  and  $\alpha_3$ ), the 3 periods ( $\gamma_1$  vs.  $\gamma_2$  and  $\gamma_2$  vs.  $\gamma_3$ ) and the upstream channel sections without fish and the downstream sections with fish ( $\delta$ ). The parameter influence on invertebrate abundance is symbolised by “▲” when the abundance increased significantly (significance probability  $\geq 0.90$ ; in bold), “=” when it did not affect the abundance ( $0.10 < \text{significance probability} < 0.90$ ) or “▼” when the abundance decreased significantly (significance probability  $\leq 0.10$ ; in bold).

	Control vs. Dry channels			Periods		Fish
	Before drying $\alpha_1$	After drying $\alpha_2$	After fish growth $\alpha_3$	Before vs. after drying $\gamma_1$ vs. $\gamma_2$	After drying vs. after fish growth $\gamma_2$ vs. $\gamma_3$	$\delta$
Diptera	=0.33	=0.68	=0.76	▼ 0.01	=0.43	▼ 0.01
Coleoptera	=0.35	=0.34	=0.74	=0.55	▲ 0.99	▼ 0.01
Oligochaeta	=0.35	=0.88	▲ 0.97	=0.60	▲ 0.91	=0.38
Others	=0.45	=0.54	=0.78	▼ 0.02	=0.76	▼ 0.01
Total	=0.35	=0.68	=0.85	▼ 0.02	=0.80	▼ 0.01



**Fig. 3.** Model estimates of the performance of juvenile trout over the 3-week growth period in the control and dry channels. Performance includes survival probability (left), growth (middle) and condition factors of juvenile trout (right). Boxplots indicate the percentiles 1, 25, 50, 75 and 99 of the posterior distributions.

while the abundance of Diptera, “Others” and the total abundance decreased ( $\gamma_1 > \gamma_2$  and  $\gamma_2 = \gamma_3$ ; Table 1 and S2).

Of the 102 juveniles used for the experiment, 95 juveniles were recovered at the end. The survival probability was similar across treatments, with a 0.92 survival rate in the control and 0.94 in the dry channels ( $\alpha = 0.418$ ;  $P(\text{Survival}_{\text{Dry}} > \text{Survival}_{\text{Control}}) = 0.65$ ; Fig. 3 and Tab. S3). In the control channels, juveniles weighed on average 1.89 g ( $\pm 1.04$ ) at the beginning and 1.88 g ( $\pm 1.10$ ) at the end of the experiment. In the dry channels, they weighed on average 1.87 g ( $\pm 0.97$ ) at the beginning and 1.86 g ( $\pm 1.11$ ) at the end. Juvenile growth in the control channels was not significantly different from growth in the dry channels ( $\alpha = -0.009$ ;  $P(\text{Growth}_{\text{Dry}} > \text{Growth}_{\text{Control}}) = 0.43$ ). In both control and dry channels, average growth was negative ( $-0.03$  and  $-0.04$ , respectively). The condition factors were also similar in control and dry channels, with average values of 0.93 and 0.92, respectively ( $\alpha = -0.012$ ;  $P(\text{Cond.Factor}_{\text{Dry}} > \text{Cond.Factor}_{\text{Control}}) = 0.31$ ).

## 4 Discussion

Hydrological anomalies are natural phenomena and more than 51–60% of the global fluvial network experiences drying

(Messenger *et al.*, 2021). However, these events are expected to intensify in the context of climate change (Skoulikidis *et al.*, 2017). Droughts and drying shape instream biological assemblages but the impacts of such events depend on the natural water regime of rivers, timing and severity (duration and intensity) of the drying disturbance, as well as the presence of refuges (Boulton, 2003). These events are extremely challenging to reproduce under experimental conditions because they strongly influence several ecosystem components (both physico-chemistry and aquatic organisms) and spatio-temporal scales. A drought crosses successive biological thresholds (reviewed in Boulton, 2003). In the beginning, the water level drops and the riparian zone is no longer connected to the main river channel. Then, river water flow stops, and the watercourse is fragmented into pools. The disappearance of surface water is the most critical stage for the fauna, leading to massive mortality. The final stage would be the water level declining in the hyporheic zone. Here, we focused on a surface water drying event, but the interstitial flow did not cease. Our results can contribute to our understanding of the impact of surface drying on trophic availability for carnivorous fish in temperate climates, as dry periods in this climatic area are usually brief, highly predictable and mostly restricted to summer (Bogan *et al.*, 2014).

In our study, the two-week surface water drying event did not alter the macroinvertebrate community. Drying events reduce the available surface habitat and connectivity between these, but macroinvertebrates can shelter in the hyporheic zone if the sediment composition allows high hyporheic permeability (Maridet *et al.*, 1992; Schmid and Schmid-Araya, 2010). Coarse gravel could provide enough inhabitable interstices to support high-density and diverse communities (Strayer *et al.*, 1997). The lack of significant effects of a drying event on macroinvertebrate abundance in our experiment could be linked to the use of the hyporheic zone as refuge. To test this idea, we would have needed to create habitats without a hyporheic zone and compare macroinvertebrate communities. We cannot be completely confident that macroinvertebrates sheltered in the hyporheic zone, but our experiment provides circumstantial evidence supporting this hypothesis.

The constant renewal of water in our experiment maintained optimum oxygen conditions in the control and dry channels (above  $11 \text{ mg L}^{-1}$  at all times; Tab. S4), which could promote the colonisation of the hyporheic zone by macroinvertebrates. In natural conditions, droughts generally increase water temperature and decrease the concentration of dissolved oxygen. For example, the temperature rose from 14 to  $25^\circ\text{C}$  and dissolved oxygen decreased from 12 to  $4 \text{ mg L}^{-1}$  during a 2-week drought in three pools in France's Albarine river (Datry, 2017), creating unsuitable conditions for many aquatic species (Vander Vorste *et al.*, 2020). Similar decreases in oxygen could be expected in the hyporheic zone, but groundwater inputs could also be involved in the physico-chemical processes occurring in the hyporheic zone. Changes in terms of dissolved oxygen in the hyporheic zone during drying events, and the consequences for the biota, are difficult to predict and site specific.

Macroinvertebrate access to the hyporheic zone depends on the permeability of the substrate. The water from the Lapitxuri and Aitzeguerra brooks does not carry large amounts of fine particles (particles  $< 2 \text{ mm}$  in size, following Wood and Armitage, 1997). These two brooks feed the Nivelles River and point measurements over 4 consecutive years near the confluence between the Lapitxuri brook and the Nivelles River revealed between 11 and 20% of fine particles in the gravel bed (Arevalo, 2014). Although we did not measure it during the experiment, the inputs of fine particles into the experimental channels were observed to be negligible. Thus, the very high permeability of the gravel bed was behind the successful colonisation of the hyporheic zone by macroinvertebrates (Stubbington, 2012). The level of fine sediments in the river bed reflects differences in land-use, geology and catchment stability (Boulton, 2003), and is increasingly recognised as a key threat to the ecological integrity of riverine ecosystems globally (Mathers *et al.*, 2017). Previous studies have demonstrated reductions in macroinvertebrate density and diversity directly induced by streambed colmatation (Descloux *et al.*, 2013; Vadher *et al.*, 2015, 2018; Mathers and Wood, 2016). Marked changes in the abundance and composition of benthic assemblages are noticeable when levels of fine particles in the streambed exceed 10% (Harrison, 2010), 20% (Zweig and Rabeni, 2001) or 30% (Bo *et al.*, 2007; Descloux *et al.*, 2013; Relyea *et al.*, 2000). Clogging homogenises benthic habitats and decreases available

spaces between larger particles, which limits permeability for most macroinvertebrates (Descloux *et al.*, 2013; Mathers *et al.*, 2014, 2019). As the hyporheic zone can contribute to resilience capacity of populations (Milner *et al.*, 2022), guaranteeing its ecological integrity is crucial with ongoing global changes (Jones *et al.*, 2012).

The persistence of macroinvertebrates during the drying event could also be related to the ecological traits of the dominant taxa. Chironomidae (Diptera) and Oligochaeta have a vermiform shape and are adapted to life in the hyporheic zone (Williams and Hynes, 1974; Stubbington, 2012). Thus, the main taxa on our macroinvertebrate communities, with taxa adapted to respond to natural flow variations, could have contributed to the limited effect of the surface water drying event observed (Naiman *et al.*, 2008). However, we also observed that the total abundance of macroinvertebrates decreased during summer, due to a large reduction in the abundance of Diptera (mainly Chironomidae). The abundance of Coleoptera and Oligochaeta increased but not enough to compensate for the loss of Chironomidae (Georgian and Wallace, 1983; Boulton *et al.*, 1992; Milner *et al.*, 2018). For macroinvertebrates, summer is often a stressful period due to low flows associated with high temperatures, diminishing total macroinvertebrate biomass both in the benthos and in the drift (Rashidabadi *et al.*, 2022). The phenology of aquatic insects, with the progressive emergence of adults of many species throughout summer could explain this reduction in macroinvertebrate abundance (Hynes, 1970; Shearer *et al.*, 2003; Baxter *et al.*, 2017). Consequently, habitat quality for stream carnivorous fish, including salmonids, could drop due to a reduction in prey availability (Rashidabadi *et al.*, 2022).

The supply of macroinvertebrates in our experimental channels was controlled with 100- $\mu\text{m}$  mesh nets and tarpaulins to focus on the dynamics of the established community. This experimental choice may also explain the gradual decline in macroinvertebrate abundance throughout summer. *In natura*, community turnover involves a range of strategies, including the drift of macroinvertebrates from upstream reaches (Datry *et al.*, 2017) and aerial dispersal (both active and passive) from perennial nearby sources (Bogan *et al.*, 2014; Sarremejane *et al.*, 2017). After droughts, 80% of the community can recover after 60 days (Pařil *et al.*, 2019), 73 days (Doretto *et al.*, 2019) or 150 days (Di Sabatino *et al.*, 2023) through these dispersal strategies. However, in a changing global context, a growing number of streams are experiencing dry periods, including perennial streams. Consequently, the effects of global change on network connectivity and the resilience capacity of systems are crucial issues. This experiment provides some evidence demonstrating that a rupture in connectivity leads to a reduction in the abundance of macroinvertebrates in isolated reaches, potentially impeding post-disturbance recolonisation.

The substrate and water velocity configuration of our channels was comparable to riffles in the Lapitxuri brook. However, riffles are suboptimal habitats for fish development in summer because of the limited delivery rate of prey (Atkinson *et al.*, 2014; Chadd *et al.*, 2017) and the energetically demanding conditions (Elliott, 2000; Lennox *et al.*, 2019). Deep pools provide more energetically favourable habitats than riffles for young-of-the-year salmonids in streams (Rosenfeld and Boss, 2001; Harvey

*et al.*, 2005; Kahler *et al.*, 2011) by limiting energy expenditure associated with swimming and station holding, while prey capture and detection rates are increased due to the concentration of prey (Nislow *et al.*, 2004). Thus, the reduction in the abundance of macroinvertebrates during summer together with the suboptimal flow conditions in the experimental channels could explain the negative performances of trout juveniles in our experiment (Sweka and Hartman, 2008).

Finally, the presence of fish significantly reduced invertebrate abundance. This phenomenon could be explained by two mechanisms. Firstly, fish can have a direct impact on invertebrates through predation. Diptera can constitute over 80% of their energy inputs (Vignes and Heland, 1995; Sánchez-Hernández *et al.*, 2012; Arevalo *et al.*, 2020), although they are opportunistic and may ingest large quantities of less favourable prey, such as Ephemeroptera and Trichoptera (Johansson, 1991). However, some groups like Coleoptera are less vulnerable to predation because of their chemical defences and unpalatability (Otto and Svensson, 1980; Keeley and Grant, 1997). Secondly, the reduction in macroinvertebrate abundance induced by the presence of fish can be explained by invertebrate predator-avoidance behaviour. Macroinvertebrates detect the chemical cues of predators and actively drift to “safe” areas with low predation pressure to minimize mortality (Muotka *et al.*, 1999; Huhta *et al.*, 2000; Naman *et al.*, 2016), which in our channel meant leaving the experimental channels.

## 5 Conclusions

In our experiment, the surface water drying event did not reduce macroinvertebrate abundance. The coarse substrate and the high water quality of the hyporheic zone probably provided sufficient refuge for macroinvertebrates. The survival and growth of salmonid juveniles were unaffected by the drying event. Our study suggests that preserving the quality of the hyporheic zone (e.g. by minimizing the inputs of fine sediment transport from the catchment to the watercourses and maintaining optimal oxygen conditions) would be key to mitigating the effects of droughts and drying on macroinvertebrates and fish.

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## Data availability statement

All files are available from the Zenodo database (doi <https://doi.org/10.5281/zenodo.10842477>).

## Supplementary materials

**Figure S1.** Water temperature (°C) recorded after the drying during trout growth (from the 16/07/2015 to the 06/08/2015) in the 3 control (black lines) and the 3 dry channels (grey dotted lines).

**Table S1.** Prior distributions assigned to parameters in the models used. E, VAR and CV correspond to mean, variance and coefficient of variation, respectively.

**Table S2.** Main statistics of the posterior probability distribution functions of the  $\alpha$  (differences between control and dry channels),  $\beta$  (all the other sources of variations, corresponding to each channel),  $\gamma$  (period) and  $\delta$  (fish predation) parameters affecting the abundance of macroinvertebrates.

**Table S3.** Main statistics of the posterior probability distribution functions of the  $\alpha$  (dry effect) and  $\beta$  (all the other sources of variations, corresponding to each channel) parameters affecting the survival, the growth and the condition factor of juveniles.

**Table S4.** Punctual measurements of dissolved oxygen concentration (in mg L<sup>-1</sup>) and water temperature (°C) during a dry event in control and dry channels.

The Supplementary Material is available at <https://www.kmae-journal.org/10.1051/kmae/2024013/olm>.

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