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Mesocosm experiments reveal the direction of groundwater-surface water exchange alters the hyporheic refuge capacity under warming scenarios.

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Running title: the hyporheic zone and climate change.

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Summary

1. Climate change is expected to affect hydrologic and thermal regimes of river ecosystems. During dry periods when river flows decrease and water temperatures increase, the hyporheic zone (HZ) can provide a refuge to surface aquatic organisms and enhance the resilience capacity of riverine ecosystems. However, shifts from up- to downwelling flow conditions in the HZ could jeopardize this capacity.
2. Using laboratory mesocosms and high resolution fiber-optic distributed temperature sensing, we explored the combined effects of 5 different increased surface water temperature treatments (from 15 to 27 ºC at 3 ºC intervals) and the direction of water exchange on the ability of *Gammarus pulex* (Crustacea, Amphipoda) to migrate into the HZ as a response to warming. We determined the survival rates of this ubiquitous hyporheic dweller and its rates of consumption of *Alnus glutinosa* leaf litter in the HZ.
3. Results showed that at increasing surface water temperature leaf litter breakdown was observed at a greater depth in the sediments under downwelling flow conditions, i.e. *Gammarus pulex* migrated deeper into the HZ compared to upwelling conditions, resulting in greater survival rates (64 ± 11 vs. 44 ± 10 %). However, under both upwelling and downwelling conditions, we found evidence for potential use of the hyporheic zone as a thermal refuge for *G. pulex*. Below sediment depths of 25 cm, temperatures remained low (< 22 °C) even when surface waters were at 27 °C, so temperatures deep in the hyporheic zone never exceeded critical thermal thresholds for *G. pulex*.
4. This study provides evidence that alterations to the direction of groundwater-surface water exchange can alter the capacity of the HZ to provide a refuge for benthic invertebrates, thereby affecting the resilience of river communities to warming under climate change.

Introduction

Significant changes in the hydrologic and thermal regimes of rivers are expected to occur under global warming (Webb & Nobilis, 2007; van Vliet *et al.*, 2013), affecting biodiversity and functioning of freshwater ecosystems (Woodward, Perkins & Brown, 2010; Ledger & Milner, 2015; Leigh *et al.*, 2015). Typical consequences include geographical range shifts in animal and plant communities (Walther *et al.*, 2002; Root *et al.*, 2003; Holzinger *et al.*, 2008), habitat loss or fragmentation (Mantyka-Pringle, Martin & Rhodes, 2012) and altered food webs interactions (Woodward, Dybkjær, Ólafsson *et al.*, 2010; Kratina *et al.*, 2012; Ledger *et al.*, 2013). As most aquatic organisms are ectotherms, they are highly sensitive to temperature increases (Sibly & Atkinson, 1994; Daufresne *et al.*, 2004; Daufresne, Lengfellner & Sommer, 2009; Vander Vorste *et al.*, 2016a). So changes to river thermal regimes alter freshwater community diversity and composition (Brown, Hannah & Milner, 2007; Datry *et al.*, 2014; Leigh *et al.*, 2016).

The hyporheic zone (HZ), defined as the saturated interstices below and adjacent to river channels (White, 1993) in which groundwater and surface water mix (Krause, Hannah, Fleckenstein *et al.*, 2011), can provide a refuge for river organisms (Palmer, Bely & Berg, 1992; Stubbington, 2012; Vander Vorste *et al.*, 2016a). Refuges, *sensu* Sedell et al. (1990), can favour the survival of many riverine species including invertebrates and fish, particularly in a context of global change (Keppel *et al.*, 2015; Ledger & Milner, 2015). Because the HZ is characterized by reduced daily and annual temperature amplitudes compared to surface water (Hannah, Webb & Nobilis, 2008; Krause, Hannah & Blume, 2011), it is a potential refuge for surface river organisms during adverse thermal conditions (Palmer *et al.*, 1992; Stubbington, 2012; Vander Vorste *et al.*, 2016a). Surface and HZ habitats are vertically interconnected by upwelling (exfiltration) and downwelling (infiltration) fluxes of water, solutes and organisms (Brunke *et al.*, 1997; Boulton, Findlay & Marmonier, 1998).

Upwelling conditions reflect water fluxes from the HZ into the surface, whereas downwelling is the infiltration of surface water into the HZ. Water temperatures in the HZ are generally lower than channel water in summer and higher in winter (Evans, Greenwood & Petts, 1995; Arrigoni *et al.*, 2008; Krause, Hannah & Blume, 2011). Therefore, the HZ represents a potential thermal refuge for surface organisms when surface temperatures become unfavourable. Early signals of *Gammarus pulex* actively using the HZ to avoid exposure to elevated temperatures (Wood *et al.*, 2010; Vander Vorste *et al.*, 2016a) or desiccation (Vadher, Stubbington & Wood, 2015; Vander Vorste *et al.*, 2016b) have been detected in natural systems. Hence, the HZ may mitigate the negative effects of climate warming on organisms resilience and associated ecosystem processes, such as organic matter decomposition (Stubbington, 2012; Kawanishi *et al.*, 2013; Vander Vorste *et al.*, 2016a).

In a climate change context, the capacity of the HZ to provide a thermal refuge may be at risk due to shifts in the direction of groundwater-surface water exchange, potentially reducing the resilience of riverine ecosystems. The combination of reduced runoff and greater demand for water resources increases human reliance upon groundwater causing increased pumping and lower groundwater levels (Green *et al.*, 2011; Treidel, Martin-Bordes & Gurdak, 2012; Taylor *et al.*, 2013). Lower groundwater tables contribute less groundwater to river base flow (Fetter, 2001; Sophocleous, 2002), altering interactions between groundwater and surface waters (Krause & Bronstert, 2007; Kløve *et al.*, 2014) and reversing conditions from upwelling to downwelling (Stanley & Valett, 1992; Dole-Olivier & Marmonier, 1992b; Dahm *et al.*, 2003). The consequences of such complex interacting pressures, (warming under climate change, more frequent and extreme events and increased groundwater abstraction), on the refuge capacity of the HZ are still poorly understood (Dole-Olivier, 2011; Stubbington, 2012). On one hand, enhanced downwelling could increase hyporheic water temperatures with heat being propagated deeper into the HZ by additional heat advection

(Boulton *et al.*, 1998; Malard *et al.*, 2002; Krause, Hannah & Blume, 2011), and this could preclude the HZ from acting as a thermal refuge during warming. On the other hand, downwelling conditions may favour the passive downward migration of aquatic organisms from the surface into the HZ and promote their survival (Dole-Olivier, Marmonier & Beffy, 1997; Stubbington, Wood & Reid, 2011). To accurately predict the response of riverine communities and ecosystem processes to climate change, it is crucial to understand how the direction of groundwater-surface water exchange, heat transport and animal behaviour interact and possibly alter the potential capacity of the HZ to act as a refuge.

In this study, we addressed the effects of change in the direction of groundwater-surface water exchange on the capacity of the HZ of gravel-bed rivers to act as a thermal refuge for surface organisms. Using laboratory mesocosms, we simulated real ranges of increased surface water temperatures, representing for instance disconnected standing pools associated with stream channel contraction, and we manipulated the direction of water exchange. We tested the following hypotheses:

1) The HZ provides a thermal refuge for river organisms when surface water temperature increases because it will remain cooler with a narrower range of temperatures than surface waters, as predicted under climate change in many riverine systems;

2) The direction of groundwater-surface water exchange mediates this refuge capacity, which will be lower in downwelling conditions than in upwelling conditions because warmer surface water flow into the HZ will raise the temperature of the HZ under downwelling conditions, but upwelling water will remain cooler than surface waters.

Methods

Experimental design

We used a set of 10 experimental mesocosms to mimic gravel-bed river HZs and simulated increased surface water temperature and reversed flow direction due to climate change. We applied 5 temperature treatments, from 15 to 27 ^{0}C, and 2 contrasting hydrological conditions, comprising upwelling (exfiltration) and downwelling (infiltration) flow (Table 1), and observed the vertical migration of *G. pulex* in response to these treatments. This amphipod was used as a model organism (see details below).

We conducted Fiber-Optic Distributed Temperature Sensing (FO-DTS) high-resolution monitoring of vertical temperature profiles and kept dissolved oxygen levels close to saturation to avoid any possible anoxia. To assess the vertical migration of *G. pulex* into the HZ we used rates of *Alnus glutinosa* leaf litter breakdown (Navel *et al.*, 2010; Vander Vorste *et al.*, 2016a; Foucreau *et al.*, 2016). The experiments ran for 15 days and were repeated 3 times (n total = 30) within a 4-month period (see details below).

Mesocosm design

The mesocosms were made of opaque PVC, 120 cm high, 25 cm in diameter and filled to the height of 90 cm with washed gravel (sediment size = 10-14 mm), to provide a substrate not limiting to the vertical migration of *G. pulex* (Navel *et al.*, 2010; Vadher *et al.*, 2015) into the HZ (Fig. 1a,b,c). Each mesocosm was divided into two main parts (Fig. 1c); a 30-cm surface zone: 10 cm at the top were left for gas exchange and 20 cm for surface water; and a 90-cm sediment zone representing the HZ. To analyse physical and chemical pore water properties, mesocosms had lateral tubing outlets every 15 cm from -5 cm from the free water-sediment interface to -80 cm depth (6 in total each), screened with 500 µm mesh to prevent *G. pulex* from escaping the mesocosms.

Temperature treatments

We generated five distinct surface water temperatures of 15, 18, 21, 24 and 27 ^{0}C to simulate climate-induced warming of rivers water (Table 2). The chosen temperature values spanned the range of temperatures observed *in-situ* (Zwolsman & van Bokhoven, 2007; van Vliet & Zwolsman, 2008) or projected for rivers in temperate regions under future climate change through modelling approaches (Mantua, Tohver & Hamlet, 2010; van Vliet *et al.*, 2013). To heat the water, we used heating cables (0.5 cm diameter) (Hydrokable, Hydor Inc. Sacramento, CA USA) placed onto the sediment surface in the free water column and coiled around the inner wall of the mesocosms (Vander Vorste *et al.*, 2016a). We controlled surface water temperature using an electronic thermostat (± 0.1 ^{0}C) (Hobby, Dohse Aquaristik GmbH & Co., Grafschaft, Germany) and kept surface water temperatures constant until the end of the experiment. A 12:12-h light:dark cycle was applied using Grolux (35 W, 8500 K, Sylvania Inc., Noida, India) aquarium lights above mesocosms. Throughout the experiment, we kept mesocosms in a temperature-controlled room (16.4 ± 0.4 ^{0}C).

Hydrological treatments

We used peristaltic pumps to generate up- and downwelling conditions. The resulting infiltration rate in the mesocosms was 1.9 L/h (Darcy velocity: 6.7 cm/h) which generated an interstitial water velocity of 22.3 cm/h. Upwelling flow was simulated by pumping continuously dechlorinated tap water (which was kept aerated by air bubblers) from a 1000-L tank into the bottom of the mesocosms (n = 5). Water drained (1.9 L/h) through a 2-cm diameter hole, screened with 500 µm mesh, located 10 cm below the top of each mesocosm. Downwelling flow was simulated by pumping water from the tank into the top of the mesocosms (n = 5) and forcing water to flow through the sediments by pumping out interstitial water from the bottom of the column (1.85 L/h), while 0.05 L/h drained trough a 2-cm diameter hole, screened with 500 µm mesh, located 10 cm below the top of each mesocosm.

In each mesocosm water volume (22.8 L) was renewed for both flow paths every 12 hours to avoid any possible hypoxia, particularly for downwelling treatments. We measured dissolved oxygen and temperature in interstitial water twice during each experimental run. They were measured at 3 depths (5, 35 and 80 cm in the HZ) by drawing interstitial water from the outlets and using a portable multi-parameter meter (HQ40D, Hach, Loveland, USA, DO resolution = 0.01 mg/L, temperature = 0.1 °C). An air bubbler kept surface water in each mesocosm aerated, and dissolved oxygen concentrations in interstitial water varied between 6.53 and 9.64 mg/L in the HZ.

High resolution temperature sensing profiles

Raman-backscatter Distributed Temperature Sensing (DTS) is being increasingly used in environmental applications including hydrological processes (Selker *et al.*, 2006) because it provides high-resolution, continuous temperature data collection in space and time (Briggs *et al.*, 2012). DTS systems provide temperature measurements along a fiber-optic cable by analysing the ratio of the amplitudes of the temperature-independent backscatter, Stokes, to temperature-dependent anti-Stokes signal of the light pulse emitted by the instrument (Selker *et al.*, 2006; Tyler *et al.*, 2009). The timing of these backscatter returns yields a measure of location (Briggs *et al.*, 2012). The precision of the measurements depends on the accuracy of Stokes/anti-Stokes ratio, and greater signal strength requires longer integration time (Selker *et al.*, 2006).

We continuously monitored vertical temperature profiles in the mesocosms for each of the 15-day experimental runs at high spatial and temporal resolution using 10 high resolution temperature sensing profiles (HRTS) (Briggs *et al.*, 2012), specifically constructed for the purpose. The DTS instrument applied was a Silixa XT-DTS (Silixa, Elstree, UK), having a sampling resolution of 25 cm, suggesting a minimal spatial resolution of > 50 cm along the fiber based on the Nyquist criterion (van de Giesen *et al.*, 2012). A small armoured bend-insensitive fiber-optic temperature sensing cable with stainless steel loose tube containing 2 optical fibers, 1.6 mm diameter (Brugg Kabel AG, Brugg, Switzerland) was wrapped around a PVC pipe (6-cm external diameter hollow PVC pipe, 1.2 m long), pre-threaded at a specific pitch, to create a HRTS with 0.004 m vertical sampling resolution. The PVC pipes were threaded along the central 1 metre of length, leaving the first and last 10 cm of the pipes unthreaded. Each HRTS was placed vertically in the centre of the 10 mesocosms. Temperature values were taken continuously every 2 minutes for the total length of the experiment. Alternate single-ended monitoring mode was adopted (Krause & Blume, 2013), and a dynamic instrument calibration was used, based on matching the temperatures of two separate sections of the fibre in a control bath. Specifically, at both ends of the fibre-optic cable, sections of > 20 metres were coiled and kept at a constant temperature in a 0 ^{0}C ice bath during the experiment (Tyler *et al.*, 2009) and their monitoring temperatures matched during calibration to account for potential drift caused by differential loss along the cable length.

The number of HRTS that could be connected in series by splicing the fiber cable together before signal loss occurred was affected by the total number of splices (Tyler *et al.*, 2009). This limited the number of mesocosms that could be employed in a single experimental run. For this reason, based on published literature (Briggs *et al.*, 2012), we limited the number of mesocosms to 10 and repeated the experiment three times using an identical design.

Model organism

We used *G. pulex* (Amphipoda: Crustacea, Linnaeus, 1758) as a biological model because of its wide distribution and abundance throughout Europe (Graça, Maltby & Calow, 1994; Macneil, Dick & Elwood, 1997). It is a facultative component of the hyporheos (Dole-Olivier & Marmonier, 1992a), able to burrow up to 2 m into deep sediments during adverse surface conditions (Dole-Olivier *et al.*, 1997; Stubbington *et al.*, 2011), is eurythermic (Foucreau *et al.*, 2014) and can tolerate moderate hypoxia for several days (Danielopol, 1989). Its crucial role in leaf litter breakdown has been well documented in streams (Graça *et al.*, 1994; Navel *et al.*, 2010; Piscart *et al.*, 2011). Together, these reasons make *G. pulex* a valuable and widely used model for laboratory and environmental change studies (Navel *et al.*, 2010; Foucreau *et al.*, 2014; Vander Vorste *et al.*, 2016a).

During the experiment, we twice collected (early March and mid-May 2016) adult amphipods of similar size (5-7 mm) from a first-order stream near Dijon, France (see Vander Vorste et al. 2016a;b for details). We kept the amphipods in a temperature-controlled room (16.4 ± 0.4 ^{0}C) and allowed them to acclimatize to temperature, water (collected from the same stream as amphipods , pH = 6.99, T = 10.4 ^{0}C, EC = 527 µs/cm) and food source in aquaria (40 x 22 x 25 cm) for two weeks before the start of the experiment (Navel *et al.*, 2010). A thermostatic water pump (TECO, Ravena, Italy) kept water temperature constant (16.4 ± 0.4 ^{0}C) and air bubblers kept dissolved oxygen concentration near saturation. We fed the amphipods with conditioned alder leaves (*Alnus glutinosa*), their most preferred food source (Graça, Maltby & Calow, 1993a; Friberg & Jacobsen, 1994; Foucreau *et al.*, 2014). At each experimental run, we introduced 120 *G. pulex* into each mesocosm (3849 individuals/m^3), representing a density occurring in natural streams (Stubbington *et al.*, 2011; Vander Vorste *et al.*, 2016a), a couple of hours before starting to warm the surface water.

Assessing *G. pulex* survival rate

We quantified the percentage of individuals alive after 15 days by elutriating the sediments of each mesocosm. Water was removed from the mesocosms, and amphipods were washed out with the water and collected using sieves (500 µm). Wet sediments were then vacuumed (Kärcher WD6 Premium, 2000 W power, 30 L capacity) and mesocosms carefully washed. Prior experiments showed that vacuuming did not kill amphipods. Mesocosm sediments were then placed into separate large plastic cases and carefully elutriated, taking small sediment portions each time. Amphipods found with eyes intact and with no signs of soft tissue breakdown were counted as alive prior to mesocosm deconstruction. Amphipods that did not meet this criterion were considered dead.

Assessing *G. pulex* vertical migration

For each mesocosm, we assessed the average depth to which *G. pulex* migrated by determining (*G. pulex* mediated) leaf litter breakdown rates at different depths in the HZ (Fig. 1c, Table 1). Alder leaves, dried at 60 C for 24 h (0.4317 ± 0.0036 g dry mass) with primary veins removed, were enclosed in 7.5 x 8-cm plastic mesh bags (0.8 cm diameter) (n = 6) and positioned in the HZ at 6 different depths for each mesocosm (Fig. 1c). The mesh size allowed amphipods to enter the bags freely and consume leaf litter. To facilitate colonization by fungi and increase leaf palability (Graça, Maltby & Calow, 1993b; Graça *et al.*, 1994), leaf bags were pre-conditioned in aerated stream water for 7 days (Suberkropp & Chauvet, 1995), before being placed into the sediments. To account for microbial leaf litter decomposition, fine mesh leaf bags (500 µm, 7.5 x 6-cm) pre-conditioned in the same way (n = 6) were placed next to the coarse mesh bags at all depths (Foucreau *et al.*, 2016). The mesh size of fine mesh leaf bags excluded *G. pulex* without limiting microbial colonization (Boulton & Boon, 1991). In the same way, we prepared and pre-conditioned 3 additional coarse and 3 fine mesh leaf bags in order to correct the initial weight for loss due to handling and leaching of soluble components within 24-h after immersion (Gessner, Chauvet & Dobson, 1999).

After each run, leaves from both coarse and fine leaf bags were dried at 60 ^{0}C for 24 h and weighed. At each depth, we calculated the net leaf litter breakdown (net LLB) rate as: (final dry coarse leaf mass - initial dry coarse leaf mass corrected for leaching) – (final dry fine leaf mass - initial dry fine leaf mass corrected for leaching).

Statistical analysis

Temperature vertical patterns in the HZ for down- and upwelling conditions

To test our first hypothesis that the HZ provides a thermal refuge for *G. pulex* when surface water temperature increases, we first explored the vertical temperature profiles for each treatment. Secondly, to evaluate whether flow direction and surface water temperature influenced differences in HZ temperature between depth 1 and depth 6 (hereafter ΔT), we used linear mixed effect models with Gaussian error distribution (LME) (Bolker *et al.*, 2009; Öckinger *et al.*, 2010). Run was considered a random effect to account for variability among runs. Temperatures were log-transformed prior to statistical analysis. Linear regressions were performed to determine the significance of the correlations among variables when interaction effects were statistically significant.

Survival rates and vertical migration of *G. pulex*

To test our second hypothesis that flow direction can impair the capacity of the HZ to provide a refuge when surface water temperature increases, we tested for differences in *G. pulex* survival rates among temperature and flow direction treatments using an LME. The percentage of *G. pulex* found alive at each run was treated as the response variable, and flow and mean surface water temperature were modelled as fixed effects. Run was considered a random effect. Percentages of *G. pulex* found alive were arcsin-transformed prior to statistical tests to meet the assumption of normality.

Subsequently, we tested for differences in vertical migrations of *G. pulex* among treatments. To do so, we first calculated a leaf litter breakdown averaged depth (D) for each mesocosm, as follows:

$$\mathrm{D} = \sum_{1}^{6}(\text{net LLB} * \text{depth}) \,/\, \sum_{1}^{6} \text{net LLB}$$

D represents the average depth (m) at which G. *pulex* mediated leaf litter breakdown (LLB) was the highest. We then fit a LME to test for differences in D among treatments. Mean D for each mesocosm calculated for each run was treated as the response variable; mean surface water temperature, flow direction and the percentage of *G. pulex* found were modelled as fixed effects. We included in the model the percentage of *G. pulex* found in each mesocosm to account for the influence of the number of amphipods found at each run on D.

All statistical analyses were performed using the nlme package (Pinheiro *et al.*, 2016) in R 3.3.1 (R Core Team, 2016).

Results

Is the HZ a thermal refuge when surface water temperature increases?

For every treatment across the 3 runs, temperature was highest in the shallow sediments of the HZ (depth 1, - 5 cm) and strongly decreased from depth 3 (- 35 cm) (Fig. 2). On average, temperature at depth 3 was below 20 °C and ranged from 15.9 ± 0.1°C (18 °C, upwelling treatment) to 19.6 ± 1.2 °C (27 °C, downwelling treatment).

Temperatures in the HZ under downwelling conditions were on average 1.1 ± 0.3, 2.0 ± 0.3, 2.5 ± 0.5 and 3.6 ± 0.5 higher for 18, 21, 24 and 27 °C treatments respectively than under upwelling conditions (one-way ANOVA, flow effect, $P < 0.01$). At 15 °C, mean temperatures in the HZ under downwelling flow conditions were not different from those under upwelling conditions (15.9 ± 0.3 and 16.0 ± 0.3, respectively). Vertical temperature profiles in the HZ varied with flow direction (Table 3, interaction factor, $P < 0.0001$).

When surface water temperature increased, ΔT increased more under downwelling (R^2 = 0.98) than upwelling (R^2 = 0.60) conditions (Fig. 3). ΔT values ranged from -0.5 to 8.1 °C (mean value: 3.7 ± 0.4 °C) under downwelling flow, and it varied from 1 to 4.1 °C (mean value: 2.7 ± 1.1 °C) under upwelling conditions.

Does the direction of groundwater-surface water exchange affect the capacity for HZ to provide a refuge?

The percentage of amphipods found alive at the end of each run varied with flow direction, but not with surface temperature (Fig. 4, Table 4). On average, 64 ± 11 % of amphipods survived under downwelling conditions, whereas 44 ± 10 % survived under upwelling conditions (Fig. 4). At the end of the experiment, the mean percentage of amphipods found dead was similar between downwelling and upwelling flow condition, 3 ± 3 and 3 ± 2 % respectively (Table 5). The mean percentage of *G. pulex* not found, presumably consumed by conspecifics (due to *G. pulex* propensity for cannibalism), was 43 ± 15 % (Table 5).

D, (leaf litter breakdown averaged depth), increased with surface water temperature (Table 4, $P = 0.012$) and varied with flow direction ($P < 0.0001$), with no significant interaction (Fig. 5, Table 4). In upwelling conditions, D ranged from 0.13 ± 0.1 (15 °C treatment) to 0.22 ± 0.05 m (27 °C treatment), with a mean value of 0.18 ± 0.1 m. In downwelling conditions, D ranged from 0.27 ± 0.0 (15 °C treatment) to 0.49 ± 0.1 cm (27 °C treatment), with a mean value of 0.37 ± 0.1 m.

Discussion

Vulnerability of aquatic organisms to global warming has been demonstrated (Verberk & Bilton, 2013; Pyne & Poff, 2017), particularly for those species occupying habitats near the limits of their thermal tolerance, (e.g. in arid regions Stewart, Close, Cook *et al.*, 2013). The identification and conservation of potential refuges has therefore become a priority (Keppel *et al.*, 2012, 2015). By manipulating surface water temperature and the direction of groundwater-surface water exchange to mimic potential climate change effects on the thermal and hydrological regime of HZs, we showed that hyporheic sediments could be a potential refuge for *G. pulex*. Specifically, we found that the survival of *G. pulex* in the HZ under the range of interstitial flow velocity tested is strongly influenced by the direction of groundwater-surface water exchange when surface temperatures increase. However, our hypothesis that downwelling flow areas provide less effective refuges compared to upwelling zones was not supported. These results challenge the current paradigm that upwelling areas provide better refuges for river invertebrates during disturbance. Although we tested the response of only one species, these results show that a more comprehensive understanding is required of the potential consequences of climate change for riverine biodiversity and ecosystem resilience and how to mitigate these effects.

The HZ acts as a thermal refuge

When the temperature of surface water increased, the resulting vertical temperature patterns in the HZ differed between up- and downwelling flow conditions. However, in all treatments the deeper hyporheic sediments remained a potential thermal refuge for *G. pulex*. It is known that the downward flow of water transports heat from the surface into hyporheic sediments (Constantz & Stonestrom, 2003), and that higher infiltration rates lead to greater advection, deeper penetration and shorter lags of thermal surface signals at a given depth (Clark, Webb & Ladle, 1999; Arrigoni *et al.*, 2008; Constantz, 2008; Krause, Hannah & Blume, 2011). In our case, hyporheic temperatures were steady and not influenced by increased surface water temperature at a depth of 80 cm. Within the range of temperatures tested, similar vertical temperature patterns under downwelling conditions have been reported from previous field studies (Constantz & Stonestrom, 2003; Vogt *et al.*, 2010; Briggs *et al.*, 2012). Upwelling conditions generally provide more stable and cooler temperatures due to upward advection of groundwater and smaller variations in sediment temperature are produced compared to downwelling conditions (Alexander & Caissie, 2003; Constantz & Stonestrom, 2003; Caissie *et al.*, 2014). Similarly, in our mesocosms, increases in surface water temperature were buffered in the shallow sediments of the HZ even at the highest temperature treatment. The simulated upwelling flow had a mean temperature of 15.3 ± 0.3 °C, which is a frequent hyporheic temperature observed *in-situ*, for example in lowland alluvial rivers in the UK (Evans & Petts, 1997; Krause, Hannah & Blume, 2011), France (Capderrey *et al.*, 2013) and within the range of temperatures observed in an anthropogenic channel in Germany (Schmidt, Bayer-Raich & Schirmer, 2006). Although heat propagated deeper into the HZ under down- than upwelling conditions, for all treatments, at sediment depths below 25 cm the hyporheic temperature was < 22°C, providing a potential thermal refuge for even the most sensitive aquatic invertebrates like Ephemeroptera (mayflies) (Stewart, Close, Cook *et al.*, 2013).

The use of the HZ by *G. pulex* when surface water temperature increases

Even when surface temperature increased up to 27°C, far above the upper limit of the thermal window for *G. pulex* (10 - 20 °C, Maazouzi *et al.*, 2011), there was no significant effect of temperature on *G. pulex* survival rate, suggesting that the HZ successfully provided a thermal refuge. *G. pulex* is known to be an active vertical crawler (Elser, 2001) and it has been found in hyporheic sediments during spates under downwelling conditions (Marmonier & des Châtelliers, 1991; Dole-Olivier & Marmonier, 1992a), low flow (Stubbington *et al.*, 2011) and drying events (Wood *et al.*, 2010). In our mesocosms, we created optimal physical conditions for observing such vertical migration behaviour because of the porous gravel matrix, the absence of fine sediments clogging interstices, sufficient interstitial dissolved oxygen concentrations and food resources available at different depths. Under both up- and downwelling conditions we found evidence that *G. pulex* used the HZ to avoid increased surface water temperatures but no evidence that these increased temperatures led to lower survival rates. This indicates that the HZ acts as a refuge under flow in both directions. In addition to the findings reported in recent laboratory studies (Vadher *et al.*, 2015; Vander Vorste *et al.*, 2016a b), this study shows that the HZ may also act as a thermal refuge under both up- and downwelling conditions and therefore its potential capacity to mitigate the negative effects of climate change on river ecosystems.

The direction of groundwater-surface water exchange flow affects *G. pulex* success in using the HZ as a thermal refuge

The direction of groundwater-surface water exchange influenced the survival of *G. pulex* and its use of the HZ. Across the temperature treatments, *G. pulex* survival rates were always higher under downwelling (64 ± 11 %) compared to upwelling (44 ± 10 %) conditions. For upwelling conditions, survival rates were in the range of those reported by Vander Vorste et al. (2016a). Surprisingly, downwelling conditions seemed to better promote the survival of *G. pulex*. This result is in contrast to the assumption that upwelling zones represent thermal refuges during unfavourable surface conditions due to the upwelling of cool groundwater (Malard *et al.*, 2002; Dole-Olivier, 2011; Stubbington, 2012).

Higher survival rates under downwelling conditions corresponded to a deeper migration into the HZ by *G. pulex* compared to upwelling conditions. The average depth at which most of the leaf litter was consumed by *G. pulex* increased with surface water temperature, but was always higher under downwelling than upwelling conditions. While higher temperatures flowing into the HZ with downwelling water triggered the vertical migration of *G. pulex* deeper into the sediments, upwelling flow seemed to constrain habitat availability resulting in more organisms occupying shallow hyporheic sediments. If available habitat was constrained to the shallow hyporheic sediments, biotic interactions might have intensified as competition for food resources (leaf litter) and space increased, and organisms were exposed to high temperatures. These factors could explain the lower survival rates found for upwelling conditions, also corroborated by the fact that the mean percentage of organisms that disappeared at the end of the experiment under upwelling was higher than under downwelling conditions; we assumed that missing amphipods were the victims of cannibalism, commonly observed when *G. pulex* is under stress (Dick, 1995; McGrath *et al.*, 2007; Vander Vorste *et al.*, 2016a).

Potentially, the relatively high hyporheic water velocities used here might have prevented *G. pulex* from moving against the flow direction in upwelling water, whilst favouring downwards migration under downwelling conditions. Interstitial water velocity was ~ 22.3 cm/h, slightly higher than the one generated in previous mesocosms experiments (Mermillod-Blondin, Mauclaire & Montuelle, 2005; Navel *et al.*, 2010; Vander Vorste *et al.*, 2016a), but in the range of those reported from field surveys (Morrice *et al.*, 2000; Gerecht *et al.*, 2011). Stubbington *et al.* (2011) hypothesized that the energetic costs for organisms of long-term position maintenance in upwelling flow could be very high and our results corroborate this hypothesis. In contrast, downwelling conditions may facilitate downwards migration. This likely helped *G. pulex* to avoid lethal temperatures at the surface in the mesocosms and facilitated access to the thermal refuge in the HZ. Consequently, the broader range of depths accessed by *G. pulex* under downwelling condition as indicated by the leaf litter breakdown rates could reveal that organisms were actively moving up and down in the HZ. Organisms might have used the flow to move deeper into the HZ to escape warmer surface temperatures, but could also have moved against the flow (positive rheotaxis) to compensate downstream drift (Hughes, 1970). This seems not to have happened under upwelling conditions, probably because of the higher metabolic costs required. In natural systems upwelling zones are often characterized by depleted dissolved oxygen levels (Dole-Olivier, 2011) which may also decrease the refuge potential of the HZ. Further exploration of the capacity of the HZ to enhance the resilience of riverine biodiversity is needed because the responses by individual species to changing climate vary depending on species traits and interacting drivers of change (Chen *et al.*, 2011), and because these results may not hold in the face of more severe warming that, even in the HZ, exceeds the thermal tolerances of organisms.

Determining the complex relationships between groundwater-surface water exchange and organismal behaviour under climate change pressure will require further analysis to advance our understanding of the use of the HZ as a refuge. Indeed, to date, most ecological research seems to have overlooked the eco-hydraulics of HZs, focusing more on how the physicochemistry and biotic interactions shape hyporheic communities. Although laboratory experiments simplify reality (*e.g.* one taxon, controlled conditions), the use of mesocosms provided useful insights for understanding organismal responses to interacting factors linked to climate change which would have been virtually impossible to disentangle in the natural environment. As a next step, the novel experimental design applied in this study can be replicated and refined to recreate more realistic mesocosms conditions (Ledger *et al.*, 2009; Stewart, Dossena, Bohan *et al.*, 2013) where for instance water quality mimics that of natural systems and thus differs between up- and downwelling conditions and sediment grain size distribution is more heterogeneous.

HZs could provide thermal refuges for some surface-dwelling organisms when vertical connectivity is efficient, enabling the HZ to contribute strongly to the survival and resilience of surface species in a changing climate. Our results indicate that downwelling conditions might promote the use of different depths of the HZ by *G. pulex* even when surface water temperatures increase up to 27 °C. However, the combination of increased temperature and shifts between up- and downwelling conditions can jeopardize this refuge capacity. These results show the need to develop a landscape perspective of the HZ in rivers (Malard *et al.*, 2002) and call for additional field surveys to gain a better understanding of how hydrological conditions, and their temporal shifts, can influence riverine communities and ecosystem resilience. Additional laboratory experiments addressing the effects of altered vertical connectivity in a context of climate change where increased surface temperature, drying events and increased biotic interactions occur represents a promising research avenue for developing efficient tools and guidelines to manage river ecosystems.

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Tables

Treatment	N^0 of levels	Labels
Flow direction	2	up down
Surface water temperature	5	15 ^{0}C 18 ^{0}C 21 ^{0}C 24 ^{0}C 27 ^{0}C
Leaf litter breakdown (LLB) in the HZ	6	Depth 1 = 5 cm Depth 2 = 20 cm Depth 3 = 35 cm Depth 4 = 50 cm Depth 5 = 65 cm Depth 6 = 80 cm

Table 1. Overview of 2 flow, 5 temperature and 6 leaf litter breakdown (LLB) treatments generated in the experiment. The surface water temperature treatments chosen represented real or projected water temperature values for rivers under global warming.

Surface water T. (°C)	Flow direction	Mean (± SD) surface water T (°C) measured (n=3)
15	up	16.4 ± 0.6
15	down	15.5 ± 0.5
18	up	17.8 ± 0.2
18	down	18.0 ± 0.1
21	up	20.7 ± 0.3
21	down	20.8 ± 0.1
24	up	23.8 ± 0.0
24	down	23.6 ± 0.1
27	up	26.6 ± 0.3
27	down	26.8 ± 0.2

Table 2. Mean value (± SD) for surface water temperature (°C) as given by the high resolution temperature sensing (HRTS) profiles for each temperature and flow direction treatment during the three experimental runs.

Dependent variable	Factor	d.f.	*F*-value	*P*-value
ΔT	Flow direction (Flow)	1	14.75	0.1465
	Mean surface water T measured (T)	1	285.16	<.0001
	Flow x T	1	49.69346	<.0001

Table 3. Linear mixed effect model (LME) analysis results for temperature differences between deep and shallow hyporheic sediments (ΔT, °C) associated with flow direction and measured mean surface water temperature and the interaction between these factors.

Dependent variable	Factor	d.f.	*F*-value	*P*-value
% *G. pulex* found alive	Flow direction (Flow)	1	131.88	<.0001
	Mean surface water T measured (T)	1	0.11	0.7407
	Flow x T	1	1.51	0.2304
Leaf litter breakdown averaged depth (D)	Flow direction (Flow)	1	31.34	<.0001
	Mean surface water T measured (T)	1	7.67	0.0118
	% *G. pulex* found	1	0.03	0.8663
	Flow x T	1	1.77	0.1988
	Flow x % *G. pulex* found	1	0.16	0.6950
	T x % *G. pulex* found	1	0.46	0.5052
	Flow x T x % *G. pulex* found	1	0.05	0.8280

Table 4. Linear mixed effect model (LME) analysis results for *G. pulex* survival rates associated with flow direction and measured mean surface water temperature and the interaction between these factors; LME analysis results for leaf litter breakdown averaged depths associated with flow direction, measured mean surface water temperature and the percentage of organisms found alive and the interactions between these factors.

Surface water T. (°C)	Flow direction	% *G. pulex* found (n = 3)		% *G. pulex* not found (mean ± SD, n = 3)
		Alive (mean ± SD)	Dead (mean ± SD)	
15	up	46 ± 5	3 ± 1	50 ± 10
15	down	62 ± 13	6 ± 4	32 ± 5
18	up	47 ± 15	3 ± 2	50 ± 15
18	down	60 ± 8	4 ± 3	36 ± 8
21	up	48 ± 14	2 ± 2	50 ± 17
21	down	69 ± 17	2 ± 1	29 ± 13
24	up	38 ± 3	2 ± 1	61 ± 14
24	down	67 ± 16	3 ± 3	31 ± 2
27	up	41 ± 9	3 ± 2	57 ± 10
27	down	63 ± 8	3 ± 1	34 ± 6

Table 5. Mean (± SD) percentage of *G. pulex* found with distinction between alive and dead organisms and mean (± SD) percentage of organisms not found for each temperature and flow direction treatment.

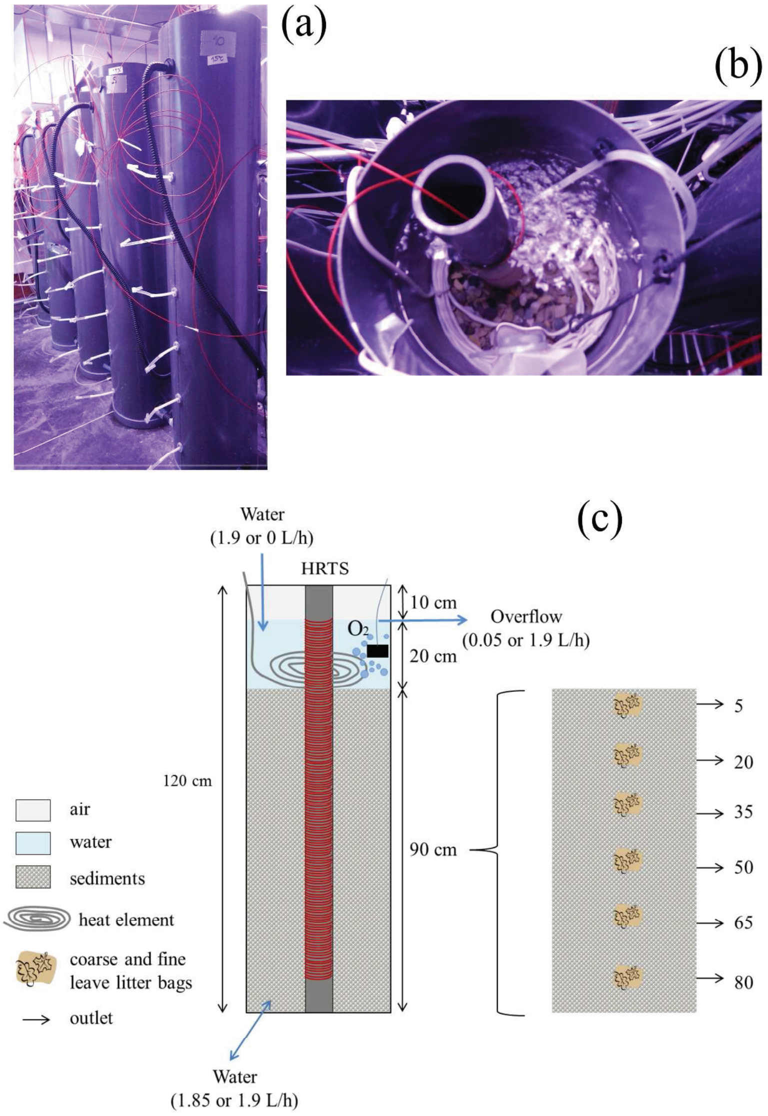

Figure 1. Mesocosm design with outside view (a), details from the inside (b) and mesocosm schematic representation indicating the dimensions of the surface and HZ, with the infiltration rates for down- and upwelling flow direction and the position of the fine and coarse leaf litter bags in the hyporheic sediments (c).

299x424mm (300 x 300 DPI)

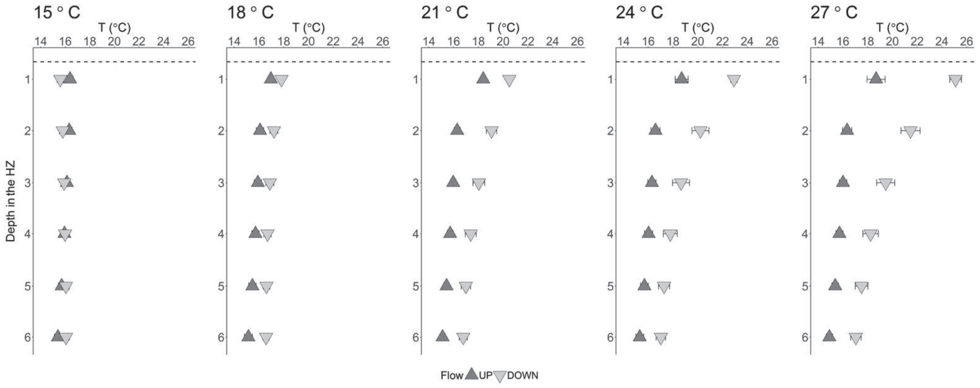

Figure 2. Mean temperature values with standard deviation (n = 3) in the HZ for both up-and downwelling flow treatments at increasing surface water temperature. Dashed horizontal line represents location of the free water-sediment interface.

152x60mm (300 x 300 DPI)

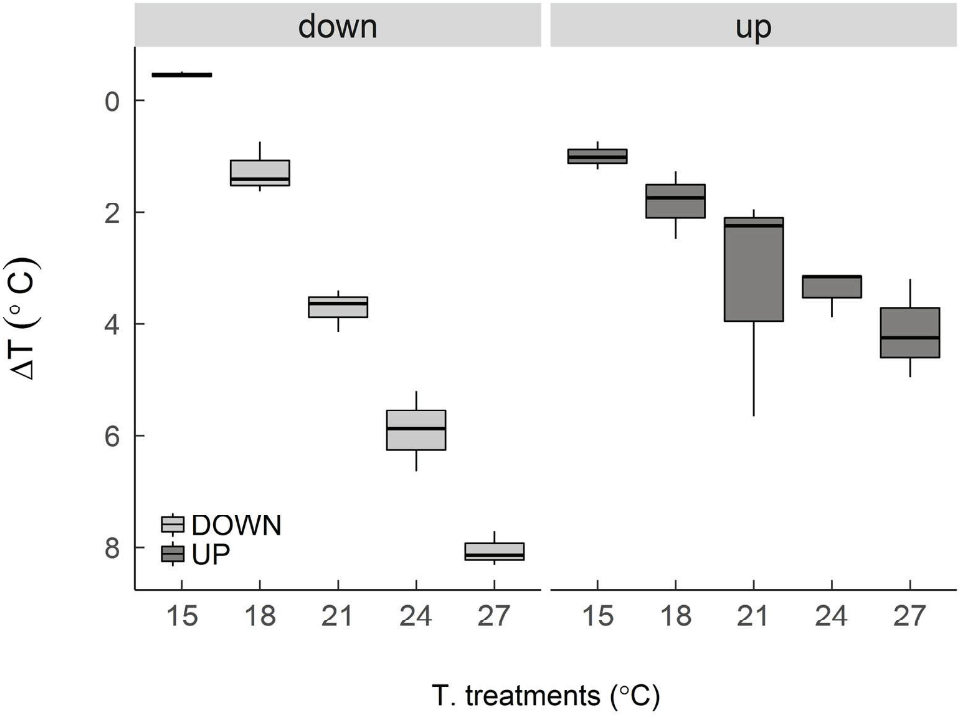

Figure 3. Median of the temperature differences (± SD) between deep and shallow hyporheic sediments (ΔT, °C) for both down-and upwelling flow conditions at increasing surface water temperature.

152x114mm (300 x 300 DPI)

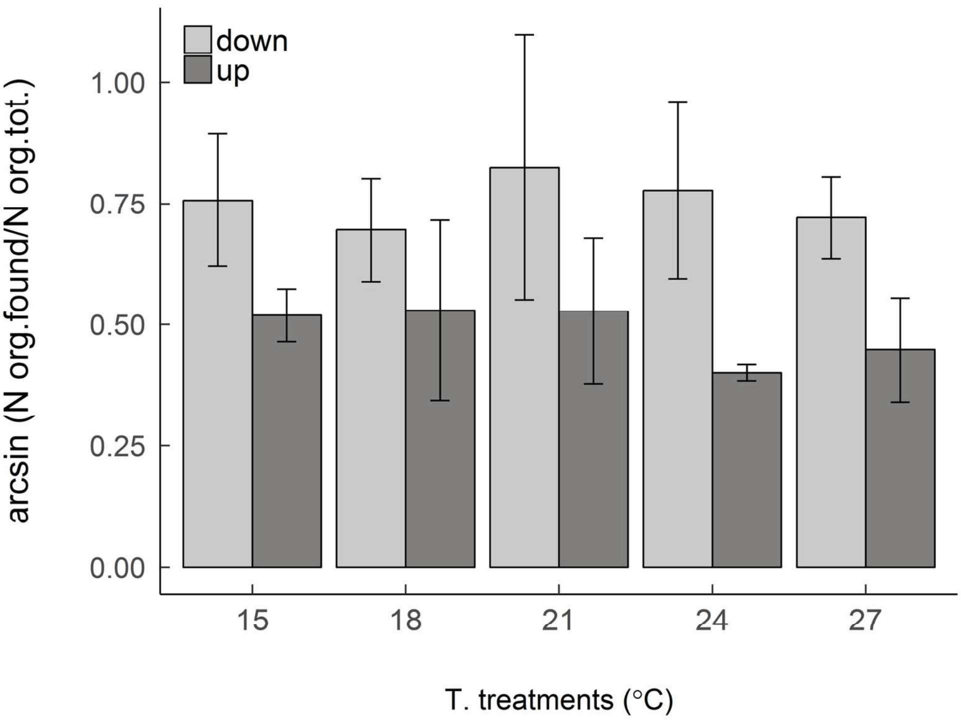

Figure 4. Mean (± SD) percentage of G. pulex found alive (arcsin-transformed) for each surface water temperature and flow direction treatments.

152x114mm (300 x 300 DPI)

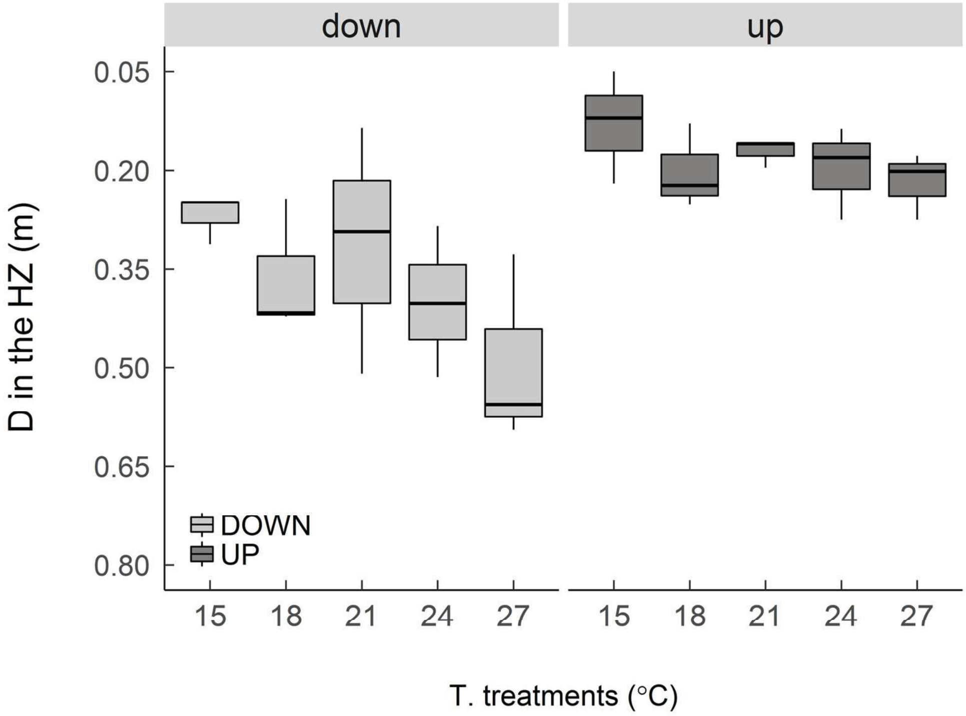

Figure 5. Median of the leaf litter breakdown averaged depths (m) for both down-and upwelling flow conditions at increasing surface water temperature.

152x114mm (300 x 300 DPI)