

**A risk assessment framework for
quantifying drought impacts on
thermal and water extremes**

by

SILVIA FOLEGOT

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ABSTRACT

Significant changes in the hydrologic and thermal regimes of rivers are expected to arise under global warming. The occurrence, intensity and duration of extreme events such as heat waves and droughts is increasing, and there is evidence to suggest that the impact of human activities is likely to interact with climate change, exacerbating the effects. Currently, the understanding of the impacts of droughts on freshwater ecosystems is still uncertain, and this is ascribed to a large degree from limitations in current sensing technologies.

By deploying Fibre-Optic Distributed Temperature Sensing (FO-DTS), this thesis aims to improve understanding of the influences of drought-induced low flows, surface water warmings, shifts between up- and downwelling flows, and hydroclimatological controls on surface water and streambed temperature dynamics. The research utilizes data collected from outdoor artificial mesocosms, data collected from laboratory-controlled mesocosms and field-based experimentation. First, the potential drought impacts on surface water and streambed temperature patterns of artificial small lowland streams are quantified. Second, high-resolution streambed sediments temperature distributions following altered groundwater-surface water exchange under distinct increased surface water temperatures are analysed. Third, the hyporheic refuge hypothesis is tested at high spatio-temporal resolution under different groundwater-surface water exchange and warming scenarios. Fourth, seasonal variability in streambed sediments temperature distributions is quantified at high spatio-temporal resolution within multiple locations in a forested stream reach in the UK. The main outcomes are: 1) surface water and streambed temperature patterns in co-evolved vegetated artificial lowland streams varied with water level, and therefore in-channel water volume; 2) the direction of groundwater-surface water exchange impacted on the transfer of thermal

stress into gravel streambeds under different warming scenarios; 3) alterations of the direction of groundwater-surface water exchange influenced the potential of the hyporheic zone of gravel streambeds to provide a refuge for *Gammarus pulex* under warming; 4) seasonal variations of streambed temperatures in a forested stream reach are primarily driven by hydroclimatological conditions.

The need to restore vertical connectivity is suggested as rehabilitation strategy to increase riverine resilience to temperature and water extremes.

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CHAPTER 1: INTRODUCTION

1.1 WATER TEMPERATURE AS MASTER VARIABLE IN A WARMING WORLD

1.1.1 TEMPERATURE AS MASTER VARIABLE

Water temperature is a determinant physical variable of aquatic ecosystems, contributing to their overall health (Caissie, 2006). It influences dissolved oxygen and other dissolved gas concentrations, conductivity and salinity as well as energetic processes associated with primary production (Friberg *et al.*, 2009), litter decomposition (Lecerf *et al.*, 2007; Gudasz *et al.*, 2010), river respiration (Sand-Jensen & Pedersen, 2005; Acuña *et al.*, 2008) and nutrient dynamics (Baron, Schmidt & Hartman, 2009; Baron *et al.*, 2013). Furthermore, water temperature controls riverine organisms' distribution, physiology, growth, timing of life-history events, synchrony of species interactions within ecological networks and ultimately survival (Durance & Ormerod, 2007; Ings *et al.*, 2009; Schabhüttl *et al.*, 2013; Verberk *et al.*, 2013). Because most river organisms are ectotherms (Durance & Ormerod, 2009), even modest changes in water temperature can have profound effects on biota across multiple level of organization (Daufresne & Boët, 2007; Woodward *et al.*, 2010a; Woodward, Perkins & Brown, 2010b).

Climate warming is currently affecting ecosystems across many regions on Earth and it is proceeding at unprecedented rates over the past 100 years (Walther *et al.*, 2002; Parmesan, 2006; Rosenzweig *et al.*, 2007; Walther, 2010). Numerous studies have provided evidence for ecological responses to ongoing temperature-related climate change (Root *et al.*, 2003; Menzel *et al.*, 2006; Walther, 2010; Richardson *et al.*, 2010; Sunday, Bates & Dulvy, 2012), with biodiversity being one of the major concerns because it is especially threatened (Hampe & Petit, 2005; Pereira *et al.*, 2010; Mantyka-Pringle, Martin & Rhodes, 2012). Freshwater

ecosystems are particularly vulnerable to climate change because they are already heavily exploited for water resources, both of surface and groundwater origin (Kløve *et al.*, 2014), and for ecosystem services (Woodward, 2009), plus they are often physically fragmented by natural and anthropogenic factors and relatively isolated within the terrestrial landscape (Woodward *et al.*, 2010b); although they cover approximately only 0.8 % of Earth's surface (Dudgeon *et al.*, 2006), fresh waters host about 6 % of all species (Dudgeon *et al.*, 2006), most of which have strong thermal regulation of growth and survival (Dixon *et al.*, 2009; Foucreau *et al.*, 2014), and limited evolutionary potential for (upper) thermal tolerance (McCullough *et al.*, 2009; but see Diamond, 2017), thus poor acclimation ability. In particular, those species with the lowest tolerance to high temperatures (Calosi, Bilton & Spicer, 2008; Durance & Ormerod, 2010) and poor respiratory control under warmer conditions (Verberk *et al.*, 2013) are most at risk from the effects of warming.

In addition, the occurrence, intensity and duration of extreme events such as floods, droughts and heat waves is increasing (Easterling *et al.*, 2000; Coumou & Rahmstorf, 2012; Garner *et al.*, 2015a; Ledger & Milner, 2015), and as a consequence changes in the hydrological and thermal regimes of rivers are expected to arise (van Vliet *et al.*, 2011, 2013). Droughts, and especially longer, unpredictable, aseasonal or supra-seasonal ones, are a major threat to both natural and human-dominated habitats (Lake, 2011) and their negative effects can be long-lasting. With the onset of a drought, stream connectivity becomes progressively disrupted by weakening or lacking longitudinal, lateral and vertical hydrological links between the stream channel and upstream habitats, the flood plain and the hyporheic zone, respectively (Lake, 2003). Falling water levels reduce the availability and heterogeneity of wet habitats, and water quality in remnant pools declines due to less riparian shading combined with high air temperatures resulting in high water temperatures and low oxygen levels (Bond, Lake &

Arthington, 2008; van Vliet & Zwolsman, 2008). The relatively high sensibility of water temperature to a strong decrease in stream discharge during dry is relevant (van Vliet *et al.*, 2011): the decrease in the volume of stream water reduces temperature buffering processes (Poole & Berman, 2001), and the decrease in flow velocity increases exposure times to atmospheric warming. Arismendi *et al.* (2013b) observed an increasing synchrony between stream temperature maxima and flow minima with a shortening in the time lag by 20-30 days between these events (e.g. earlier timing of flow minima); the less lag between these stressful events means a shortened period of relief for aquatic biota. Significant warming trends, with the highest rates of warming during the summer, have been detected or projected in previous studies (Isaak *et al.*, 2012; Ficklin, Stewart & Maurer, 2013; Basarin *et al.*, 2016), and this is generally attributed to the effects of the largest air temperature increases added to the largest discharge decreases during the summer (Moatar & Gailhard, 2006; Isaak *et al.*, 2012). Significant warming trends for monthly stream temperature minima during the summer have also been found (Arismendi *et al.*, 2013a). For example, a higher frequency and longer duration of warm-water periods with increases in summer daily minima and associated decreases in range is relevant to fish as increases in daily minima might not provide a sufficient amount of recovery time after elevated daily maxima (Johnstone & Rahel, 2003). It has been demonstrated that drought-induced increased water temperatures act on communities, populations and individuals by modifying life history, species composition, growth and reproduction (Daufresne, Lengfellner & Sommer, 2009; Friberg *et al.*, 2009; Woodward *et al.*, 2010a; Ledger *et al.*, 2012).

Under this scenario, it is therefore evident how water temperature plays and will continue playing a key role in river ecosystems biodiversity and functioning with potential implications for aquatic biota in the future, and it is therefore worthy of study and better understanding.

1.1.2 HEAT TRANSFER IN STREAMS AND STREAMBED SEDIMENTS

Heat is transferred continuously between surface water, underlying sediments and groundwater, whenever a temperature difference is present between two points along a flow path (Constantz, 2008). Typically, heat is traced by continuous monitoring of temperature patterns in the stream and streambed (Constantz & Stonestrom, 2003). Measurements of temperature gradients in the sediments in combination with measurements of hydraulic gradients are necessary to estimate heat and water fluxes exchanged at a site as well as hydraulic conductivity values (Constantz, 2008). Temperature is indeed a robust, inexpensive and immediately available parameter to monitor (Constantz, 2008), and examination of temperature patterns can give both qualitative and quantitative descriptions of a stream flow regime (e.g. gaining vs. losing water stream reaches). Heat transfer within streams and rivers occurs by a combination of radiation, conduction, convection and advection (Webb & Zhang, 1997), and these heat transfer mechanisms can add or remove heat to/from a river, giving rise to dynamic spatio-temporal stream temperature patterns (Constantz, 2008). Energy gains occur by incident shortwave (solar) and longwave (downward atmospheric) radiation, condensation and friction against the bed and the banks. Losses may occur by reflection of solar radiation, emission of long wave radiation and evaporation. Sensible heat transfer may cause gains or losses. Finally, tributary inflows, precipitations, hyporheic exchange and groundwater-surface water interactions also need to be considered. Incoming solar radiation adsorbed by the stream and/or streambed surface is responsible for radiative heat transfer, heat conduction is the direct transfer of thermal energy from warmer areas (e.g. the streambed surface) to cooler areas (e.g. the underlying sediments); heat convection occurs when water flows above streambed sediments of different temperature, and lastly, advection is the transport of heat by flowing water through the streambed sediments (Constantz, 2008). The

definitions above given make it evident that while heat conduction is present from the stream surface down to any depth in the streambed sediments – at any depth z the amplitude of the temperature fluctuation is smaller than the amplitude of the surface temperature fluctuation by a factor $e^{-z/d}$, where d is the damping depth, a characteristic depth at which the temperature amplitude is reduced to $1/e$ (Hillel, 1998) – heat advection only occurs in the streambed where flowing water is found (Constantz, 2008). Therefore, in the case of a dry streambed, the thermal signal from radiant heating and cooling of the streambed travels into the profile by conduction since advective heat transfer is virtually absent (Blasch, Constantz & Stonestrom, 2007). As this signal propagates into the sediments, its amplitude decreases and its time lag increases with respect to the surface forcing, due to heat absorption and travel time (Constantz, 2008). The modulation of the temperature variation with depth is controlled by the volumetric heat capacity of the sediments (Constantz, 2008) which is dependent on their composition and bulk density, and it increases linearly with the water content (Constantz & Stonestrom, 2003). While dry streambed-surface temperature may have a larger diurnal magnitude, below the shallowest sediments the combined effects of lower thermal conductivity and lower thermal diffusivity values for dry materials compared to saturated soils – thermal diffusivity is the ratio of thermal conductivity to volumetric heat capacity, a measure of how quickly a change in temperature is transferred to the sediments – and the lack of significant advective heat transport result in negligible diurnal variations (Constantz, 2008). For example, 15 cm is the typical damping depth for diurnal fluctuations in sandy soils (van Wijk & de Vries, 1963). Because the thermal conductivity of sediments is approximately independent of temperature but varies with water content, increasing saturations result in an increased thermal diffusivity, thus a faster and deeper propagation of a thermal signal into the profile (Blasch *et al.*, 2007). But, conversely, the hydraulic properties of streambed sediments

depend on temperature: because of the inverse temperature dependencies of both water viscosity and water density, hydraulic conductivity increases with increasing temperature; however, despite the great temperature sensitivity of hydraulic properties, the water content is still the dominant factor (van Genuchten, Leij & Lund, 1989). Streambed hydraulic conductivity in turn controls the relative importance of conduction *vs.* advection within the streambed sediments (Menichino & Hester, 2014): increasing hydraulic conductivity increases heat advection, as hydraulic conductivity largely controls both infiltration and the propagation of the thermal signal. It is well known that hydraulic conductivity is a dynamic attribute, variable in both space and time (Storey, Howard & Williams, 2003; Genereux *et al.*, 2008): because of this, any processes that can induce changes in hydraulic conductivity will modify heat transfers mechanisms in streambed sediments. For example, when bed disturbances are rare like during drought conditions, a well-developed clogging layer of finer-sized particles at the surface of the streambed will lead to continual lowering of hydraulic conductivity even in coarse sediment size, reducing connectivity between surface water and the hyporheic zone (Stewardson *et al.*, 2016). Altogether, these factors (water content and hydraulic conductivity, together with temperature sensitivity of water properties) change as a result of the seasonal variability of a stream flow regime, and control spatio-temporal variability of streambed heat transfer mechanisms, with climate change and droughts being expected to escalate and exacerbate these modifications.

1.1.3 FIBRE-OPTIC DISTRIBUTED TEMPERATURE SENSING AS A NOVEL TECHNOLOGY FOR MONITORING WATER TEMPERATURE

The study of river water temperature has a long history and technological developments with the advent of low-cost, accurate and reliable temperature sensors have made the measurement and monitoring of river temperatures easier (Webb *et al.*, 2008). Detailed temperature distributions of rivers can in fact provide important insights into the dynamics and processes controlling temperature (Selker *et al.*, 2006a), and in particular precise measurements in both space and time can help quantifying these processes (Constantz, 1998).

Fibre-optic distributed temperature sensing (FO-DTS) for use in hydrological applications provides the opportunity for continuous surveillance of streams; unlike traditional thermistors or thermocouples that would need to be individually calibrated over the measurement period, with FO-DTS it is possible to collect synchronized temperature measurements kept calibrated using one single procedure (Vogt *et al.*, 2010; Briggs *et al.*, 2012). And most importantly, DTS offers an exceptional spatial and temporal sampling resolution (Tyler *et al.*, 2009) that enables hydrologists to reveal diurnal patterns even in systems with modest amplitude of signal input, and to locate with a high spatial resolution for example longitudinal discontinuities due to groundwater inputs (Selker *et al.*, 2006a), otherwise difficult to obtain with point-wise measurements.

Raman-backscatter based DTS systems provide temperature measurements along a fibre-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.*, 2006b; 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.*, 2006b). DTS systems are relatively user-friendly (Selker *et al.*, 2006b; van de Giesen *et al.*, 2012), however instruments need to be calibrated for signal attenuation and temperature offset to obtain accurate temperature data (Tyler *et al.*, 2009). Fibre-optic cables for DTS studies can be deployed in a number of different configurations, with single- and double-ended measurements being the most common ones. In applications where the seasonal or short term variability such as the diurnal variability (e.g. Chapter 2 and 5), or in systems characterized by small-scale variability with discrete temperature signals for which a high accuracy of the FO-DTS monitored temperature patterns is required (e.g. Chapter 3 and 4), Krause & Blume (2013) proposed a combination of the advantages of both single- and double-ended monitoring mode by adopting a two-way single-ended monitoring mode. More precisely, surveys are carried out with alternating forward and backward measurements along the same fibre likeways in double-ended measurements, however, temperature offset and signal drift are corrected individually for both measurement directions similar to single-ended monitoring mode, and only after this the drift-corrected traces are averaged during data post processing (Krause & Blume, 2013). In this way, the achieved higher accuracy of signal detection especially for small-scale peak temperature anomalies (e.g. Chapter 3 and 4) and for discontinuous temperature peaks (e.g. Chapter 2 and 5) results to be particularly suited to assess potential drought impacts on riverine temperature patterns and to adequately identify both spatial and temporal complexity of highly heterogeneous systems. For this reason, FO-DTS technology in single-ended mode with alternating measurement directions was deployed in all surveys constituting the research chapters of this thesis.

Summarizing, main benefits of FO-DTS technology are:

- A single fibre can replace thousands of unsynchronised traditional temperature loggers;
- Fibre-optic cables are relatively low cost;
- Optimum DTS unit performance is maintained over a broad range of operating temperatures (from -40 to +65 °C);
- Installations can be temporary or permanent;
- Continuous measurements in both space and time allow to detect, visualize and locate sudden temperature changes in real-time;
- Very high resolution and long cables can provide high density coverage of a system;
- Fine spatial resolution and high accuracy of signal detection allow evaluating both spatial and temporal complexity of highly heterogeneous systems.

In particular, DTS modified configurations by wrapping the fibre around a pipe (Selker *et al.*, 2006b; Vogt *et al.*, 2010; Briggs *et al.*, 2012) allow to greatly increase spatial resolution, transferring the spatial resolution along the fibre from ~1 m to a vertical resolution of 0.014 m in the best case known so far (Briggs *et al.*, 2012). This fibre-optic high-resolution temperature sensors type (hereafter HRTS) can be installed vertically into the streambed, so that the temperature profile along the fibre is transformed into a depth profile (Vogt *et al.*, 2010). The resulting data set from the use of HRTS application in the hyporheic zone permits high resolution quantification of streambed temperature distributions in space and time, and it is expected to be extremely powerful to assess drought impacts on streambed sediments (up to ~1 m depth). Hyporheic exchange flows can in fact occur at very fine scales, typically centimetre-scale, induced by small bedforms, and are known to follow shallow flow paths that are typically smaller than the stream depth (Boano *et al.*, 2014). Furthermore, both hydraulic

conductivity and porosity decrease with depth in the streambed and this is determinant for controlling hyporheic flow depths and residence times (Cardenas & Jiang, 2010). The resulting heterogeneous small-scale temperature distributions within shallow depths in the streambed need therefore to be investigated using high-resolution temperature sensors, able to capture the whole complexity of vertical temperature patterns. This detailed information may be used for example to inform river managers of surface water temperature thresholds and hydrological conditions under which streambed sediments can effectively buffer surface thermal stress, to assess the impact of woody debris driving seasonal variability in streambed sediments temperature distributions, and is essential to identify with a high degree of certainty potential thermal refuge for biota under drought conditions. The use of HRTS has been previously reported only in Vogt *et al.* (2010) and Briggs *et al.* (2012). Within this thesis, HRTS were deployed for the research described in Chapter 3, 4, and 5. The vertical sampling resolution of here used HRTS was 0.004 m, to date the best resolution achieved in this type of application.

1.2 RESEARCH GAPS

Europe is one of the regions where the greatest increases of water temperature for river basins are projected, and decreases in river flow (reduced thermal capacity), particularly in summer, contribute to exacerbate the sensitivity of river water to warming (van Vliet *et al.*, 2013). The UK is no exception (Garner *et al.*, 2014a; Garner, Hannah & Watts, 2017; Orr *et al.*, 2015), with a maximum warming of between 1.2-1.4 °C for mean water temperature predicted (van Vliet *et al.*, 2013). Climate change may also impact on groundwater recharge (Green *et al.*, 2011; Treidel, Martin-Bordes & Gurdak, 2012), and an indication of a change has been

observed in the UK already (Jackson, Bloomfield & Mackay, 2015). Considering the strategic role of groundwater in moderating river temperature response to the impacts of climate change (Hannah & Garner, 2015) or other anthropogenic impacts (Mellina *et al.*, 2002) and its potential to ameliorate the effects of even more severe droughts on both surface and groundwater systems (Maxwell & Kollet, 2008; Jackson *et al.*, 2015), it is evident how an improved understanding of changes in the hydrological and thermal regimes of rivers and riverine biota responses is required. And this needs to be considered within a holistic framework that considers rivers and streams as *a three-dimensional mosaic of surface-subsurface exchange patches over multiple spatial scales* (Malard *et al.*, 2002).

The research presented in this thesis seeks to improve our knowledge of potential climate change-induced drought impacts on river thermal and hydrological regimes at different spatio-temporal scales, by deploying FO-DTS as main tool for monitoring water and streambed temperatures, and in particular by utilizing HRTS in three out of four research chapters. Research is conducted in outdoor artificial mesocosms (Chapter 2), in laboratory-controlled conditions (Chapter 3 and 4) and in a field setting (Chapter 5). Following a detailed evaluation of the literature that is presented in Chapters 2-5, four main research gaps are identified:

1. *What are the potential drought impacts on surface water and streambed temperature patterns of small lowland streams?*

Different drought conditions scenarios are simulated using three outdoor artificial streams in which water level is regulated separately and aquatic vegetation is co-evolved with the different water levels; the resulting highly variable spatial and temporal patterns of surface water and streambed temperatures are identified and quantified (Chapter 2);

2. *How are streambed temperature dynamics varying at contrasting groundwater-surface water exchange under warming scenarios?*

Thermal stress propagation is assessed in gravel streambed sediments of ten laboratory mesocosms in which the direction of groundwater-surface water exchange is modified (e.g. up- and downwelling flow) and different warming scenarios are simulated (Chapter 3);

3. *Is the hyporheic zone a refuge for surface aquatic organisms under warming scenarios?*

The potential refuge capacity of simulated hyporheic zones of gravel bed rivers is tested using ten laboratory mesocosms under five distinct surface water warmings, under different groundwater-surface water exchange, and the vertical migration together with survival rates of *Gammarus pulex* in the hyporheic sediments assessed (Chapter 4);

4. *Are streambed sediments of a forested stream buffering seasonal changes in thermal and hydrological dynamics?*

The driving processes and conditions that generate seasonal changes in streambed sediments temperature distributions across multiple locations in a lowland forested stream reach in the UK are determined and changes quantified (Chapter 5).

1.3 AIM AND OBJECTIVES

In light of these research gaps, the primary aim of this thesis is to improve understanding of the potential influences of climate change on hydrological and thermal regimes, and possible associated biotic responses, of temperate streams within a European context.

To address each of the identified research gaps, the objectives of the research are to:

1. To quantify potential drought impacts on surface water and streambed temperature patterns of small lowland streams. Improve understanding of the influence of different drought conditions severity controls on surface water and streambed temperatures of shallow streams is require to predict the thermal regime of these common streams in the future; this knowledge may be used by river managers and other stakeholders (e.g. water companies) to assure that an adequate water quality environment is maintained during drought by adopting an ecosystem approach to managing water (Chapter 2);
2. To analyse at high resolution streambed sediments temperature distributions following altered groundwater-surface water exchange under distinct increased surface water temperatures. Interactions between modifications in the hydrological and thermal regimes during warming and resulting temperature distributions in streambed sediments need be investigated at high spatio-temporal resolution; this information is essential to preserve natural micro-heterogeneity of streambed sediments temperatures under a changing climate (Chapter 3);
3. To test the hyporheic refuge hypothesis under different groundwater-surface water exchange and warming scenarios at high spatio-temporal resolution. The hyporheic zone represents a potential thermal refuge for some river organisms when surface water becomes adverse due to warming. However, in a climate change context this capacity may lessen. And considering the importance of identifying cold refuges from climate change for the persistence of species it is straightforward to imagine that such research may contribute to yield new insights as to the potential of the

hyporheic zone to mitigate the negative effects of climate change on organismal and ecosystem resilience (Chapter 4);

4. To quantify seasonal variability in streambed sediments temperature distributions at high spatio-temporal resolution within multiple locations in a forested stream reach. The assessment of the magnitude of seasonal cooling/warming patterns driven by varying hydroclimatological conditions is fundamental to acquire knowledge of the *in situ* conditions under which streambed sediments are effective in buffering river thermal extremes under present and future climate pressures (Chapter 5).

1.4 THESIS STRUCTURE

The research presented in this thesis follows a paper-style format with each chapter being an independent self-contained piece of research (Chapter 2-5). Within each chapter, the relevant literature is reviewed and a detailed description of methods is included as well. To avoid repetitions, when the same methods are adopted then the reader is referred to relevant chapter where the methods are first described in detail. All chapters are indeed linked by a common research methodology that is FO-DTS, Chapters 3-5 by a particular DTS application that is HRTS. A synthesis of the main findings together with future research suggestions are presented in Chapter 6. Figure 1 provides a schematic outline of the thesis.

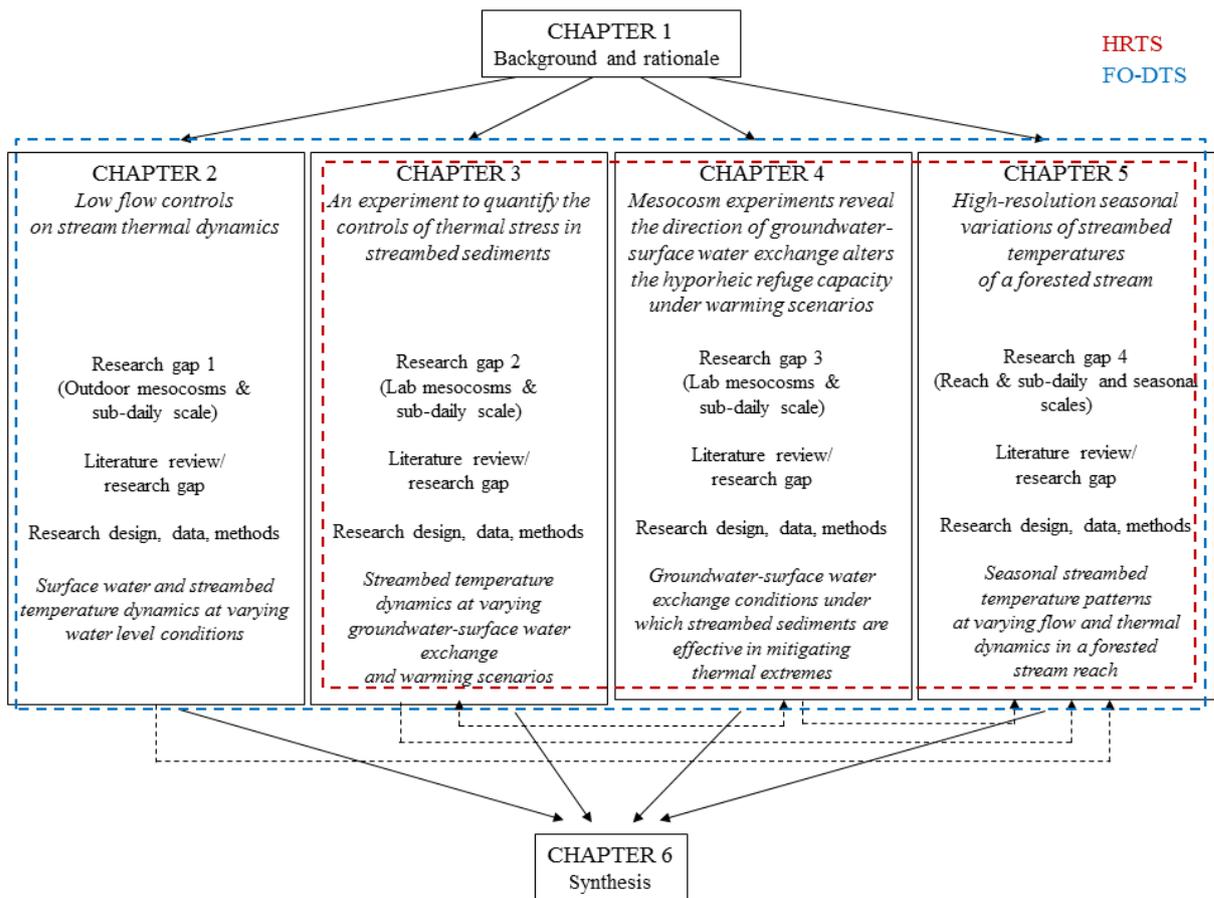


Figure 1. Overview of the thesis structure. Arrows show inter-relationships between chapters.

CHAPTER 2: LOW FLOW CONTROLS ON STREAM THERMAL DYNAMICS

2.1 INTRODUCTION

Temperature is a master water quality variable driving physical, chemical, and biological processes in aquatic ecosystems by directly influencing metabolic rates, physiology and life-history traits of aquatic organisms, as well as their abundance and distribution (Webb, 1996; Constantz, 1998; Bogan, Mohseni & Stefan, 2003; Caissie, 2006; Webb *et al.*, 2008). Stream water temperature is dynamic over space and time (Poole & Berman, 2001), and is influenced by numerous natural variables and eco-hydrological processes, including solar radiation, air temperature, heat transfer at the air-water interface, precipitation, riparian vegetation shading, surface water inflows, and groundwater and streambed heat exchanges (Constantz, 1998; Bogan *et al.*, 2003; Johnson, 2004; Arrigoni *et al.*, 2008; Webb *et al.*, 2008; Garner *et al.*, 2015b; Hannah & Garner, 2015). In particular, the streambed, identified as an important heat source and sink (Evans, McGregor & Petts, 1998; Hannah *et al.*, 2004), can significantly affect the river's energy budget both temporally and spatially (Evans *et al.*, 1998), influencing water column temperatures. Natural temporal fluctuations in surface and streambed water temperature are observed on a diel and annual cycle (Caissie, 2006), while spatially, temperatures generally increase along the longitudinal dimension. However, discontinuities, both of natural and anthropogenic origin can interrupt the longitudinal thermal profile (Fullerton *et al.*, 2015). At the micro-scale, morphological in-stream structures like riffle-pool sequences create spatial temperature heterogeneity, supporting diverse communities and providing refuge from extreme temperatures, especially during summer (Hester, Doyle & Poole, 2009; Dallas & Rivers-Moore, 2011). Although temperature variations occur naturally, river flow and thermal regimes have been profoundly altered by both climate change and human interventions, e.g. dams and water withdrawals, on the hydrological cycle (Döll & Zhang, 2010; Schneider *et al.*, 2013; Laizé *et al.*, 2014), with potential severe impacts on

freshwater ecosystems and biodiversity (Bates *et al.*, 2008; Bond *et al.*, 2008; Poff & Zimmerman, 2010; Vörösmarty *et al.*, 2010).

Extreme climatic events have recently received attention (Easterling *et al.*, 2000; Garner *et al.*, 2015a; Ledger & Milner, 2015; Leigh *et al.*, 2015) because of the growing awareness that they may cause dramatic changes to river and streambed temperature regimes (Jentsch, Kreyling & Beierkuhnlein, 2007; Palmer *et al.*, 2009). Droughts, in particular, can lead to a decrease in flow permanence (Lake, 2003), fragmenting the water course into pools (Boulton, 2003), possibly drying the streambed, and reducing longitudinal connectivity (Bogan, Boersma & Lytle, 2015). As a consequence of these drought effects, water quality generally declines and surface water temperatures increases (Matthews, 1998). As most aquatic organisms are ectotherms (Giller & Malmqvist, 1998), and thus, are sensitive to increases in water temperatures (Daufresne *et al.*, 2009), understanding how water level fluctuations control river and streambed thermal regimes has become indeed a matter of urgency to assure aquatic ecosystem integrity and functioning.

Water depth together with discharge and velocity directly influences and regulates the distribution and growth of aquatic flora (Riis & Biggs, 2003; Franklin, Dunbar & Whitehead, 2008; Bornette & Puijalon, 2011). Macrophyte communities play a key role in unshaded streams (Riis & Biggs, 2003) by increasing physical and biological diversity, and by contributing to habitat structure and ecological functioning of these systems (Warfe & Barmuta, 2006; Thomaz & Cunha, 2010). While stable flows favour macrophyte biomass (Mebane, Maret & Simon, 2014), the increased number and frequency of hydrological disturbance events, such as floods and droughts, can significantly alter the composition and abundance of aquatic macrophyte communities (Riis & Biggs, 2001, 2003; Stromberg *et al.*, 2005), causing biomass destruction, and habitat structure change (Grime, 1979). Under this

constraint, plant species with a greater resistance and/or resilience usually dominate (Riis *et al.*, 2008), whereas others, such as *Ranunculus* species, only occupy channel areas with permanent flow (Westwood *et al.*, 2006). As a result, during droughts, the channels of ephemeral or perennial streams experiencing severe drying can be invaded and colonized by resistant and/or amphibian or riparian plant species (Bunn & Arthington, 2002; Lake, 2003), a process called terrestrialization (Holmes, 1999; Westwood *et al.*, 2006). Strictly aquatic macrophytes (Schuyler, 1984) and non-aquatic forms possess different shading abilities that are quite influential for both water and streambed temperatures. Non-aquatic forms in particular, being characterized by more competitive growth forms (e.g. tall or broad-leaved species; Bornette & Puijalon, 2011), have highly variable shading effects on surface water and streambed sediments. Therefore, water level fluctuations due to drought conditions can influence aquatic vegetation coverage and indirectly, stream temperature regimes. However, to our knowledge, no previous high spatio-temporal resolution studies of the combined impact of both water level and vegetation coverage on temperatures at the channel bed and in the water column have been carried out.

Direct *in situ* studies of water level impacts on the thermal regime of natural channels can be challenging technically and logistically because of their high spatial and temporal complexity. The use of distributed fibre-optic monitoring solutions allows for the possibility to investigate stream thermal regimes continuously in both time and space (Selker *et al.*, 2006a; Tyler *et al.*, 2009). In this way, high spatial and temporal stream temperature variability can be detected, resulting in improved monitoring and assessment of stream thermal regimes. Manipulating water levels in a flume experimental set-up allows for the isolation and alteration of the key variables of interest under controlled conditions, although at a smaller physical scale (Mosley & Zimpfer, 1978).

Given the research gaps outlined above, the aim of this study is to analyse the combined effect of water level variation and co-evolved vegetation coverage on the streambed and surface temperature patterns of artificial rivers. By using three outdoor flumes, representative of characteristic lowland gravel-bed rivers with developed plant communities, the potential drought (e.g. water level) impacts on the downstream warming of surface water and spatial patterns of streambed surface temperatures are assessed continuously for the duration of the study.

The following hypotheses are tested:

- I) surface water warming is inversely associated with water depth, with temperatures in the deeper flumes being more effectively buffered by both the water column and broader co-evolving vegetation coverage than in shallower flumes;
- II) spatial temperature patterns are more pronounced in the shallowest flume with extreme temperature values (maximum and minimum streambed and surface water temperature values) varying more than average temperatures;
- III) the impact of meteorological variability, especially changes in air temperature and solar radiation, are more marked for shallower water depths.

2.2 METHODS

2.2.1 SITE DESCRIPTION

The experiment used three outdoor flumes at Fobdown Watercress Farm, near New Alresford, Hampshire, U.K. ($51^{\circ}06'08.57''\text{N}$, $1^{\circ}11'06.33''\text{W}$, 99 m asl; Figure 2).

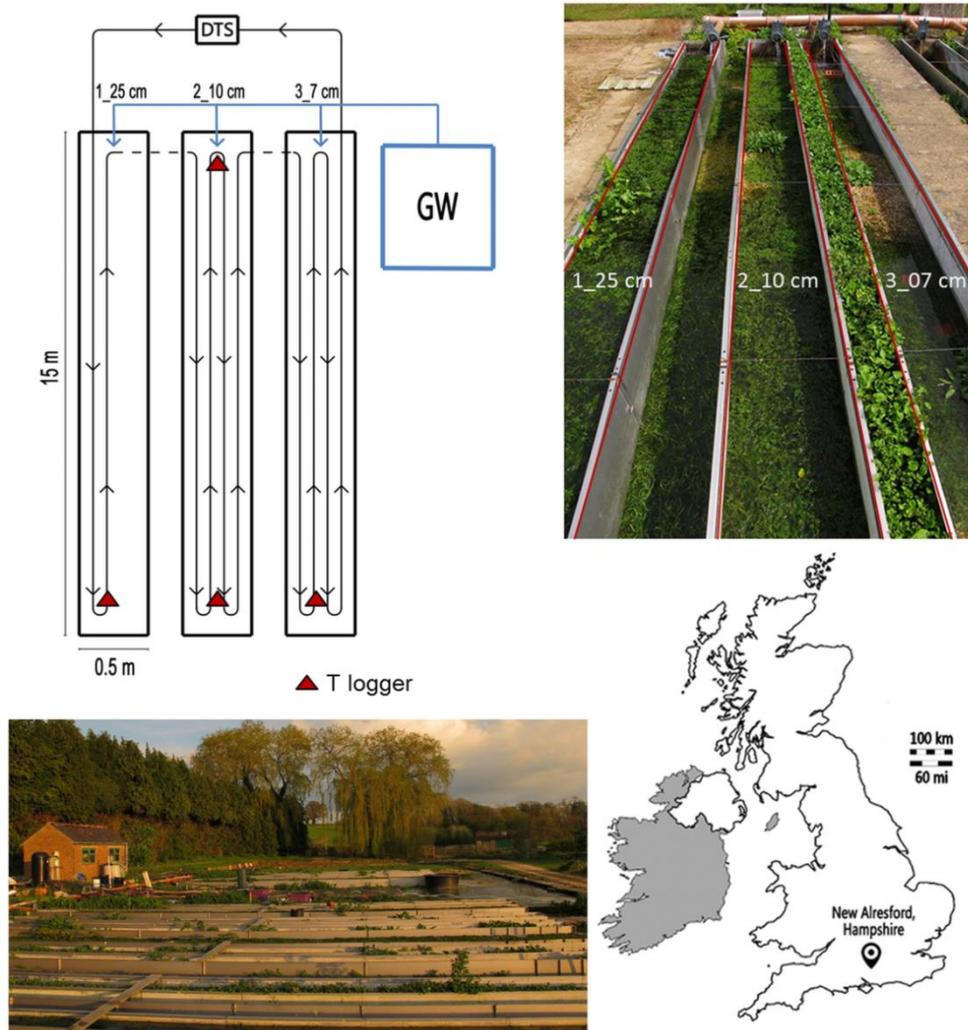


Figure 2. Description of the experimental set up, pictures of the flumes and location of the study area.

The experiment ran from $\sim 16:00$ 23-04-2014 to $\sim 14:00$ 25-04-2014. Average air temperature for the month of April was 10.0°C (Alice Holt Lodge UK Met Office weather station, ~ 30 km away from study site), with a peak of 17.5°C on the 21-04-14. The minimum of 2.1°C

was registered the 24-02-16. Daily average precipitation was 0.2 mm with a maximum of 13.4 mm on the 25-04-14 (Figure 3).

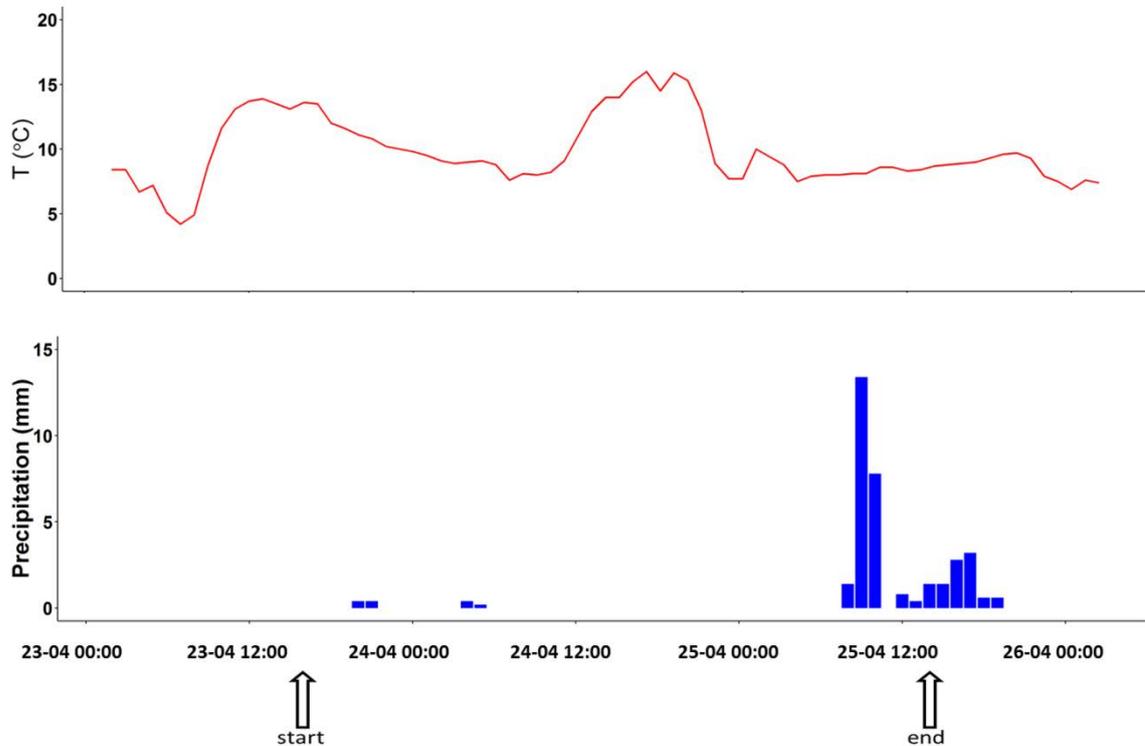


Figure 3. Temperature (°C) and precipitation (mm) at the site over the duration of the experiment (source: National Centre for Atmospheric Science, Natural Environment Research Council, Met Office Integrated Data Archive System).

The aluminium flumes had dimensions of 15 m length and 0.5 m width, with walls of 0.5 m (Figure 2). Water supply for the flumes was provided from a groundwater well with a constant temperature of 10.1 °C. Water quality parameters (temperature, electric conductivity and dissolved oxygen) were monitored continuously to ensure stationary water quality boundary conditions throughout the experiment. Groundwater (GW) was pumped at a constant rate into a feeder tank of 80 L capacity, from where it was subsequently distributed to the flumes using a network of pipes. Different water levels were obtained by regulating the water intake and outflow for each flume separately, and water levels in the pools were set to 25, 10 and 7 cm in the three flumes, respectively (flumes are hereafter referred to as ‘1_25

cm’, ‘2_10 cm’ and ‘3_07 cm’). The three water levels were representative of different levels of drought severity, with flume 1_25 cm representing close to normal flow conditions for southern UK chalk streams, flume 2_10 cm summer low flow conditions and 3_07 cm severe drought conditions. Steady state conditions were maintained throughout the experiment.

The flumes were all filled with a bottom layer of washed sediments (particle sizes: 80% 11-22 mm; 12% 2-11 mm; 6% 0.35-2 mm; 2% <0.35 mm; Table 1) to create identical pool-riffle-pool sequences along the length of the flume (Poynter, 2014). Sediment thickness measurements were taken at 0.35 m intervals longitudinally and every 0.10 m across the flumes width, starting at 0.35 m from the upstream boundary and finishing at 14 m (39 sampling points along and 5 across to cover a global area of 7.25 m² per flume). Water depths in the flumes were calculated by subtracting the flume-averaged depth to water and the sediment thickness at each grid cell from the total flume wall height.

Table 1. Particle size distribution in flume sediments.

Particle size (mm)	Percentage (%)
< 0.35	2
0.35 - 2	6
2 - 11	12
11 - 22	80

Vegetation in the flumes was introduced artificially using ~ 10 cm 5-rooted fragments of *Ranunculus penicillatus* subsp. *pseudofluitans* spaced at 2 m intervals, and was allowed to evolve naturally since the flumes’ installation in August 2013. *Ranunculus penicillatus* subsp. *pseudofluitans* (Syme) S.D. Webster, is a divergent, fine-leaved, submerged aquatic macrophyte, typically found in English chalk streams where it is generally the dominant species. At the time of the experiment, the flumes’ vegetation represented a climax community that had developed for 8 months after flume installation according to the water

level present in each flume. The vegetation cover (%) during the experiment was estimated by photo surveys taken every 1.5 m along the flumes.

Sediment thickness, water depth and vegetation coverage surveys were interpolated using Ordinary Kriging in ArcGIS (ESRI, 2011). Interpolations of all three spatial parameters (sediment thickness, water depth and vegetation coverage) resulted in rasters of 1.9 cm grid cells. These data were further analysed using the Spatial Analysis toolbox in ArcGis (ESRI, 2011) to evaluate spatial patterns in average, variance, minimum and maximum temperature ranges and as well as spatial correlations between parameters (using Band Collection analysis).

2.2.2 SURFACE WATER TEMPERATURE MONITORING

Temperature data loggers (MiniDot oxygen and temperature loggers, PME, San Diego USA, ± 0.1 °C accuracy) were installed in flowing water in the last pool of the pool-riffle-pool sequences at the end of each flume at the sediment-water interface and programmed to monitor surface water outflow at 10-minute intervals (Figure 2). The loggers were fully submerged. When vegetation was present, this protected them from direct solar radiation; when not (only for the shallowest flume), the loggers' white colour (high albedo) meant that they were unlikely to have been affected (Johnson & Wilby, 2013). Another temperature logger (LTC Levellogger Junior, Solinst, Georgetown Canada, ± 0.1 °C accuracy) was installed in the vegetation mats and fully submerged in the first pool of the pool-riffle-pool sequence at the start of the second flume to continuously monitor inflow surface water temperature in minute intervals. As the physical properties of the inflow water were temporally stable and did not vary among flumes, it was assumed the use of a single logger was representative of inflow water for all flumes. All temperature loggers monitoring inflow and outflow water

temperatures were inter-calibrated before the start of the experiment. The pool-riffle-pool sequences helped to reduce water stratification and to maintain vertical mixing, especially in the shallow flumes where riffles produced rapid flow in contrast with deeper pools (Richards, 1976). In addition, large and dense aquatic macrophytes blockages represent obstacles to the flow, resulting in turbulent mixing that resembles that generated by the fast flow of a riffle (Green, 2005). Therefore, a blockage across the flume by macrophytes could be seen as being a pseudo-riffle (Green, 2005). Spot surveys confirmed that surface water temperatures did not stratify.

Analysis and processing of data were performed using the R statistical computing and graphic environment (R Core Team, 2013).

2.2.3 STREAMBED WATER TEMPERATURE MONITORING

To investigate spatial patterns of streambed temperature continuously at high spatio-temporal resolution, FO-DTS technology was applied along a complex geometrical setup (Figure 2). In recent years, distributed temperature sensing technology based on Raman backscatter from fibre-optic cables has been widely adopted for extensive environmental applications (Selker *et al.*, 2006b; Tyler *et al.*, 2009; Briggs *et al.*, 2012; Krause *et al.*, 2013; Sebok *et al.*, 2015). The measurement principle of FO-DTS is based on the analysis of the backscatter properties of a light pulse emitted from the DTS unit that travels through an optical fibre. The observed ratio of Stokes/anti-Stokes backscatter is used to quantify temperature at high sampling resolution (up to 12.5 cm) along fibre-optic cables (up to several km in length). Measurement precision depends on distance from the light source and on the integration time, so points further from the DTS unit have fewer photons observed and will need greater integration times to achieve desired precision (Selker *et al.*, 2006b). Assuming robust calibration procedures, DTS

systems with 1 m spatial resolutions along cables of up to 5 km have been reported to provide precision of the order of 0.1 °C for integration times of 60 seconds (Selker *et al.*, 2006b; van de Giesen *et al.*, 2012).

Table 2. FO-DTS coverage of flume surfaces: number of FO-cable transects per flume, max length per cable transect per flume (m) and discarded points per transect per flume (*For 1_25 cm FO-cable transects started 1 m downstream).

Flume	DTS cable transect	DTS cable transect length (m)	Points discarded
1_25 cm	2	13.7*	8+5
2_10 cm	4	13.5	11+13+8+5
3_07 cm	4	12.7	0+2+6+3

For the experiment, a fibre-optic cable was deployed at the sediment surface water interface of the three flumes using a double-looped configuration as indicated in Figure 2. For flume 1_25 cm, 2 transects of FO-DTS cable were deployed at the streambed surface (cable failure in the second loop), whereas for flume 2_10 cm and flume 3_07 cm, 4 transects were used. The cables were fixed to the streambed using flat stones to keep them in position. Nevertheless, exposure of the cable to the air could not be completely prevented, particularly in the shallowest sections. Sections of data where the cable detached from the sediment surface were discarded and considered as missing values (NAs) in the subsequent analysis. Similarly, the most up-stream and down-stream measuring points where the cables entered and exited the flumes (which may have been influenced by air temperature), were excluded from the data analysis. The number of points that had to be discarded for each transect varied between different DTS sections among flumes (Table 2). Because of the presence of a cable coil at the upstream end of the flume, the most upstream DTS sampling point taken into consideration for flume 1_25 cm was 1 m further downstream than in the other two flumes.

The fibre-optic cable applied in this study was a 2-multimode fibre stainless-steel tube with 1.32 mm outside diameter (AFL Telecommunication, Hawksworth, UK); the two bend insensitive 50- μm multimode fibres were bedded in a gel, and the stainless-steel tube (SS 304) was not encapsulated. An ULTIMA-S TM (Silixa, Elstree, UK) DTS instrument was used with a sampling resolution of 12.5 cm that offers a spatial resolution as fine as 30 cm. FO-DTS monitoring was carried out in single-ended mode with alternating measurement directions of the light pulse as described in Krause & Blume (2013) in order to preserve the best possible resolution of the spatial temperature patterns. To account for signal drift and offset a dynamic calibration was defined (Hausner *et al.*, 2011) and for this, \sim 15 m reference sections of the fibre-optic cable were installed in a constant temperature ice bath. To avoid preferential heat transport, the cable was fully covered with iced water; cable contact with the walls of the ice container was avoided throughout the experiment. Temperature measurements were averaged at 30-second intervals for the duration of the experiment, this means that the time interval between measurements from the same channel was one minute. Streambed temperature data were analysed using the package *matrixStats* (Bengtsson, 2015) of the statistical software R (R Core Team, 2013) and daily mean, variance, minimum and maximum temperatures were obtained for each sampling day and plotted using the *ggplot2* package (Wickham, 2009).

2.3 PREDICTIONS OF SURFACE WATER TEMPERATURE VARIATIONS

In order to ensure that observed changes in surface water temperature between the inflow and outflow in each of the flume were in line with theoretical expectations, and not due to solar

warming of the instrumentation, a simple Lagrangian deterministic approach similar to that described by Garner *et al* (2014b) was used to model water temperature within the flumes. Equations used to compute heat inputs due to solar radiation, net longwave radiation, latent heat and sensible heat were derived from those given in Boyd and Kasper (2003). As input meteorological data was not available directly on-site, input meteorological parameters were collected from the nearest (~ 30 km) UK Met Office weather station, located in Southampton (Met Office, 2006). The model calculates the temperature of a parcel of water of 0.126 m (length equal to the chosen spatial resolution of the DTS instrument) by 0.5 m (width equal to the width of the flume) as it moves through the flume. The model assumes that water within the flume is well mixed. Simplified streambed morphology was assumed and depth was the averaged depth in each flume (Table 3). The residence time of each parcel within the flume was ~5 hours. Vegetation coverage was not taken into account. Water parcels were ‘released’ on an hourly basis for the period 23-04-14 16:00 to 24-04-14 13:00, and the temperature of each parcel computed hourly as it transited the flume. The magnitude of warming of a parcel was computed by subtracting the modelled temperature of water at the outflow of the flumes from the inflow (inflow temperature given by the temperature data logger placed in the first pool in flume 2_10 cm). The rate of predicted changes was used to confirm that observed variations were in line with theoretical expectations.

2.4 RESULTS

2.4.1 SEDIMENT AND WATER DEPTH

Sediment thickness and water depths for the three flumes are shown in Figure 4 A and B.

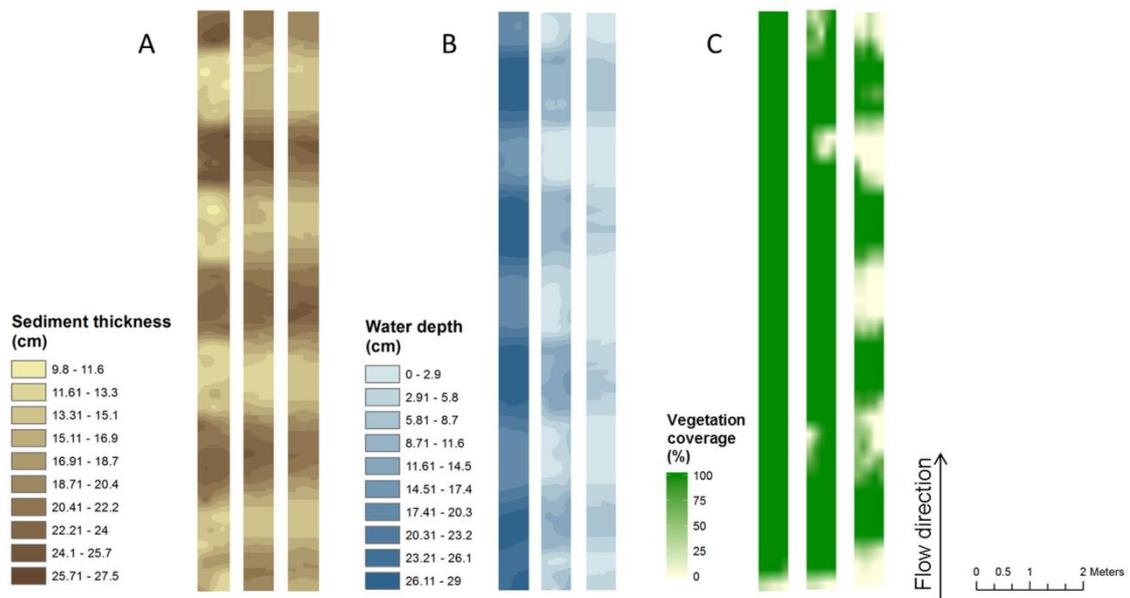


Figure 4. Spatial distribution of A) sediments thickness (cm), B) water depth (cm) and C) vegetation coverage (%) in the flumes. The pool-riffle-pool sequences are clearly visible in the sediment and water depth distribution and echoed in the vegetation coverage.

The average sediment thickness of each of the flumes was 17.6, 18.6 and 17.8 cm for flumes 1_25 cm, 2_10 cm and 3_07 cm, respectively. Average flume water depths were 23.4, 7.1 and 3.4 cm for flumes 1_25 cm, 2_10 cm and 3_07 cm, respectively (Table 3). The pool-riffle-pool sequences formed by the sediments in the flumes comprised 4 pools per flume with an average water depth of 27.2, 11.1 and 6.1 cm for flumes 1_25 cm, 2_10 cm and 3_07 cm, respectively. All sediments were submerged in flume 1_25 cm, while 0.05 m² of sediment was exposed to the air in flume 2_10 cm (0.7% of the total flume surface area) and 0.52 m² (7.2% total area) was exposed in flume 3_07 (Table 3).

Table 3. Flume average sediment thickness (cm) and volume of sediment (m³), average water depth (cm), pool water depth (cm), discharge (x 10⁻⁴ m³/s), velocity (x 10⁻² m/s) and volume of surface water (m³), proportion of sediment surface exposed to the air (m²) with relative percentage to total flume area (%).

Flume	Sediment thickness (cm)	Volume of sediment (m³)	Water depth (cm)	Pool water depth (cm)	Discharge (x 10⁻⁴ m³/s)	Velocity (x 10⁻² m/s)	Volume of surface water (m³)	Area of exposed sediment (m²)
1_25 cm	17.6	1.3	23.4	27.2	13.00	1.11	1.7	0.00 (0.0%)
2_10 cm	18.6	1.4	7.1	11.1	4.77	1.37	0.5	0.05 (0.7%)
3_07 cm	17.8	1.3	3.4	6.1	0.38	0.22	0.3	0.51 (7.2%)

2.4.2 VEGETATION COVERAGE

Vegetation coverage in the 3 flumes is shown in Figure 4 C. Total vegetation coverage for flume 1_25 cm was 96.7% (7.01 m²), including 95.3% coverage by aquatic vegetation (*R. pseudofluitans*) and 1.38% by emergent herbaceous plants. Un-vegetated areas consisted of open water, mainly near the flume inlet. In flume 2_10 cm, total vegetation coverage was 90.6% (6.57 m²), including 88.6% aquatic vegetation and 2.1% terrestrial cover. The remaining un-vegetated area consisted of a small area of bare sediments (0.05 m², 0.7% of total area) and of shallow surface water (0.63 m², 8.7% of total area). In flume 3_07, the total vegetated cover was only 4.07 m² (56% of total area), including 51.5% aquatic vegetation and 4.5% non-aquatic plants. Bare, exposed sediments covered a surface area of 0.52 m² (7.2% of the total area), and un-vegetated water made up the remaining 2.67 m² (36.8% of total area). Spatial correlation using Band Collection analysis between vegetation coverage (without distinction between strictly aquatic and non-aquatic forms) and water level rasters within each flume revealed no correlation for flume 1_25 cm, increasing to 0.46 ($P < 0.001$) for flume 2_10 cm and 0.85 ($P < 0.001$) for flume 3_07 cm.

2.4.3 INFLUENCE OF WATER DEPTH ON SURFACE OUTFLOW TEMPERATURES

Water entering the flumes had a constant temperature of 10.1 °C (± 0.07 °C) throughout the duration of the experiment (Figure 5 A). Mean (\pm standard deviation) of surface outflow temperatures recorded by the temperature loggers placed at the end of each of the flume was 10.5 \pm 0.1, 10.5 \pm 0.1, 10.5 \pm 0.2 °C for flumes 1_25 cm, 2_10 cm and 3_07 cm respectively on 23-04-14, 10.7 \pm 0.5, 10.7 \pm 0.4, 11.1 \pm 1.1 °C for flumes 1_25 cm, 2_10 cm and 3_07 cm

respectively on 24-04-14 and 10.5 ± 0.2 , 10.4 ± 0.2 , 10.4 ± 0.4 °C for flumes 1_25 cm, 2_10 cm and 3_07 cm respectively on 25-04-14.

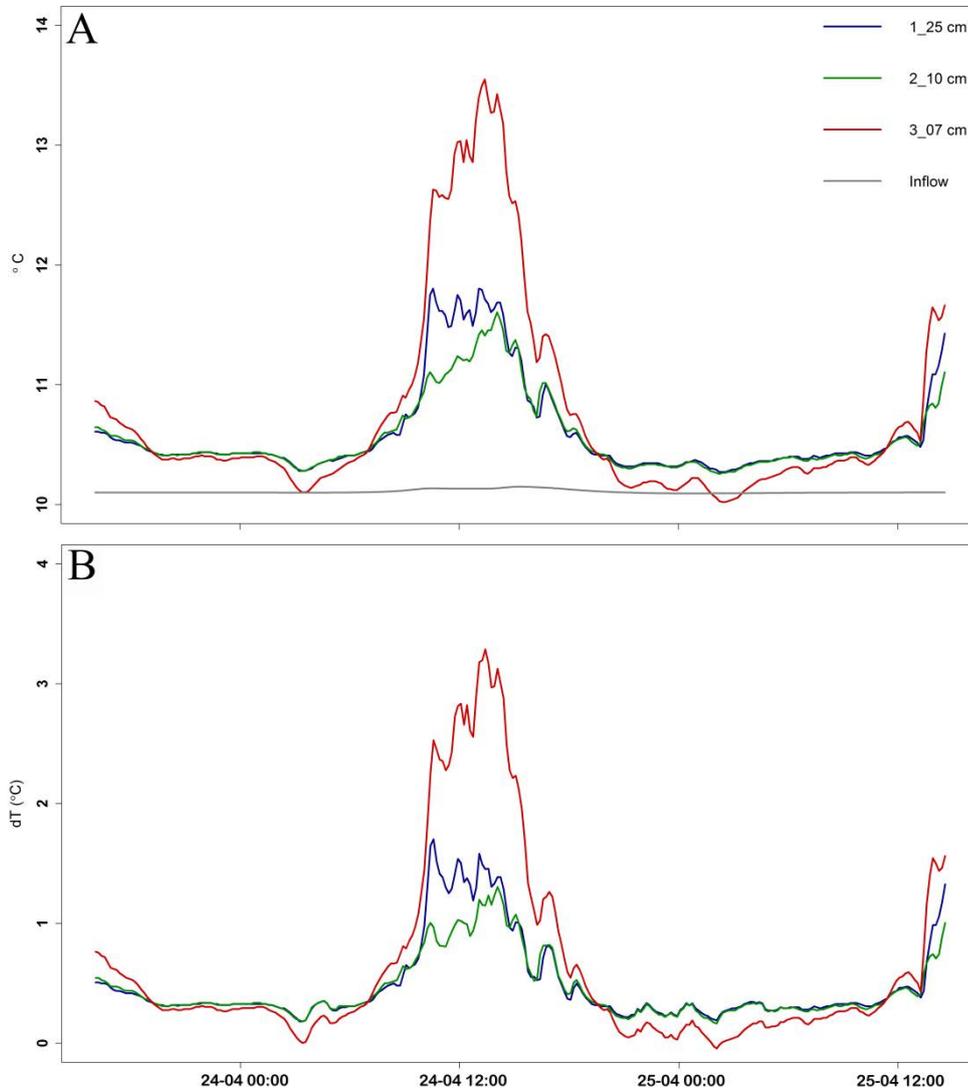


Figure 5. Surface water temperature measured at the inflow in flume 2_10 cm and at the outflow of the three flumes (A) and difference between inflow and outflow temperatures (B).

Surface outflow temperatures were more consistent among the different flumes during low insolation (23-04-14 and 25-04-14), and varied more when solar radiation was high (24-04-14) (Table 4). Diurnal variability in outflow temperatures was highest in the shallowest flume, 3_07 cm, with the overall lowest temperature being recorded at night (10.0 °C around 02:30 on 25-04-14) and the highest during the day (13.5 °C around 13:30 on 24-04-14; Figure 5 A).

A Kruskal Wallis test revealed a significant effect of flume on surface outflow temperatures registered at 10-minute intervals throughout the experiment ($\chi^2 = 9.7$, $P < 0.01$). A post-hoc test using Mann-Whitney tests with Holm correction showed no significant differences between surface outflow temperatures registered for flume 1_25 cm and for 2_10 cm, but significant differences between those measured for flume 1_25 cm and 3_07 cm ($P < 0.01$, $r = 0.12$).

Table 4. Daily averages for air temperature (°C), global solar irradiation (KJ/m² d), flume average outflow surface water temperatures with standard deviation and range values (minimum-maximum) for 23-04-14, 24-04-14 and 25-04-14 (*Data taken from Southampton meteorological station, about 30 km distance).

Day	Air T (°C)	Global solar irradiation (KJ/ m ² d)*	T 1_25 cm out (°C)	T 2_10 cm out (°C)	T 3_07 cm out (°C)
23-04-2014	10.2	8280	10.5±0.1 (10.4-10.6)	10.5±0.1 (10.4-10.6)	10.5±0.1 (10.4-10.9)
24-04-2014	10.9	19640	10.7±0.5 (10.3-11.8)	10.7±0.4 (10.3-11.6)	11.1±1.1 (10.1-13.5)
25-04-2014	8.5	3580	10.5±0.2 (10.3-11.4)	10.4±0.2 (10.3-11.1)	10.4±0.4 (10.0-11.7)

The magnitude of surface water temperature change (defined as the temperature difference between surface water inflow and outflow; δT) varied in both space and time. Maximum warmings of 1.7, 1.3 and 3.3 °C for flumes 1_25 cm, 2_10 cm, 3_07 cm respectively were all observed in the daytime of 24-02-14 (Figure 5 B). The most intense warming (3.3 °C; flume 3_07) was experienced at 13:30. The lowest magnitude temperature changes were observed at night-time. While δT for flume 1_25 and 2_10 cm was always positive (minimum outflow surface water was 0.2 °C warmer than inflow for both flumes), the outflow temperature for flume 3_07 cm was generally the same as the inflow temperature, and sometimes cooler than it (-0.04 °C; 25-04-14 at 02:00). The magnitude of warming simulated using the simple temperature model described in section 2.3 matched observed data. Assuming that global solar irradiation recorded at Southampton for 24-04-14 (a clear-sky day) was similar to the

study site, absolute simulated warmings reached the maximum of 0.6, 1.8 and 3.5 °C in flumes 1_25 cm, 2_10 cm, 3_07 cm respectively (compared to absolute maximum observed warmings of 1.7, 1.3 and 3.3 °C for flumes 1_25 cm, 2_10 cm, 3_07 cm respectively).

2.4.4 STREAMBED WATER TEMPERATURES

Spatial patterns of streambed temperatures calculated for each sampling point along the DTS transects were pronounced and varied significantly in the three flumes and between the different sampling days (Table 5).

Table 5. Mean with standard deviation and range values for average, variance, minimum and maximum streambed temperature patterns for each flume during the experiment.

Date	Flume	Avg. T (°C)		Var. T (°C)		Min. T (°C)		Max. T (°C)	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
23-04-14	1_25 cm	10.5±0.0	10.5-10.6	0.0±0.0	0.0-0.0	10.2±0.0	10.0-10.3	10.9±0.1	10.8-11.1
	2_10 cm	10.5±0.0	10.4-10.6	0.0±0.1	0.0-0.4	10.1±0.1	9.4-10.2	11.0±0.2	10.7-12.0
	3_07 cm	10.5±0.0	10.3-10.6	0.1±0.1	0.0-0.7	10.0±0.2	9.3-10.3	11.2±0.4	10.7-12.9
24-04-14	1_25 cm	11.0±0.1	10.9-11.2	0.3±0.1	0.1-0.8	10.1±0.1	9.9-10.2	12.2±0.4	11.6-13.3
	2_10 cm	11.0±0.4	10.5-12.9	1.2±2.9	0.0-19.4	9.9±0.5	7.1-10.2	13.0±2.3	11.0-24.3
	3_07 cm	11.0±0.5	10.6-12.8	2.8±5.1	0.0-24.0	9.5±0.9	6.8-10.3	14.4±3.9	11.2-27.1
25-04-14	1_25 cm	11.0±0.0	10.9-11.1	0.1±0.0	0.0-0.1	10.6±0.1	10.2-10.7	13.0±0.1	12.8-13.2
	2_10 cm	10.6±0.3	9.0-11.1	0.1±0.1	0.0-0.8	10.1±0.6	7.1-10.7	12.8±0.2	12.4-13.3
	3_07 cm	10.2±0.4	8.8-10.6	0.1±0.2	0.0-0.8	9.5±0.9	6.7-10.2	11.8±1.0	10.2-13.1

During 23-04-14, daily average streambed temperature ranged from 10.5 °C to 10.6 °C for flume 1_25 cm, from 10.4 °C to 10.6 °C for flume 2_10 cm, and from 10.3 °C to 10.6 °C for flume 3_07 cm (Figure 6 A), with a mean daily value along and across all flumes of 10.5±0.0 °C. The magnitude of streambed temperatures changes on 23-04-14 was generally limited (Figure 6 B, C and D) and this was particularly true for flume 1_25 cm. However, despite the limited magnitude of temperature change, a significant downstream increase in maximum streambed temperatures for flume 1_25 cm was still evident (Kendall's test, $\tau = 0.36$, $P < 0.001$). Greater spatial temperature variability was more evident in the areas of the shallower flumes where aquatic vegetation coverage was sparser and/or sediments were exposed.

The warmest and most variable streambed temperatures across the 3-day study were observed on 24-04-14, a relatively warm, clear-sky day (Table 4). Average temperature values calculated for 24-04-14 and over space exhibited relatively high variability, ranging from 10.9 °C to 12.2 °C for flume 1_25 cm, from 10.5 °C to 12.9 °C for flume 2_10 cm, from 10.6 °C to 12.8 °C for flume 3_07 cm (Figure 6 E), with a daily mean value of 11.0±0.4 °C across and along all flumes. On 24-04-14, flume 3_07 cm was the one to exhibit the most extreme streambed temperature values; in fact, variance in flume 3_07 cm ranged from 0.0 to 24.0 °C (Figure 6 F) due to different warming and cooling gradients between vegetated vs. un-vegetated shallow water areas and bare exposed sediment features. The greatest response to increased global solar irradiation receipt for 24-04-14 for flume 3_07 cm resulted in a daily maximum streambed temperature registered that was 2.8 °C warmer than the maximum in flume 2_10 cm and 13.8 °C warmer than the maximum recorded in flume 1_25 cm (Figure 6 H). Similarly, minimum streambed temperatures for flume 3_07 cm exhibited a more intense night cooling compared to the deeper flumes: minimum streambed temperature values were in

fact 0.4 °C and 3.1 °C colder than those of flume 1_25 cm and 2_10 cm, respectively (Figure 6 G).

The lowest streambed temperatures coincided with heavy rain and colder air temperature on 25-04-14. The absolute lower limit of minimum streambed temperature ranges for the shallower flumes (2_10 and 3_07) was registered on 25-04-14 (Figure 6 M), while absolute maximum streambed temperature values for these flumes were approximately half of those recorded during clear-sky conditions (24-04-14) (Figure 6 N). In contrast, flume 1_25 cm was less responsive to the change in meteorological conditions compared to the shallower flumes. Absolute minimum streambed temperatures for flume 1_25 cm were higher on 25-04-14 than on 24-04-14 (10.2 °C and 9.9 °C respectively), whereas absolute maximum streambed temperatures did not vary substantially between 24-04-14 to 25-04-14 (13.3 and 13.2 °C respectively).

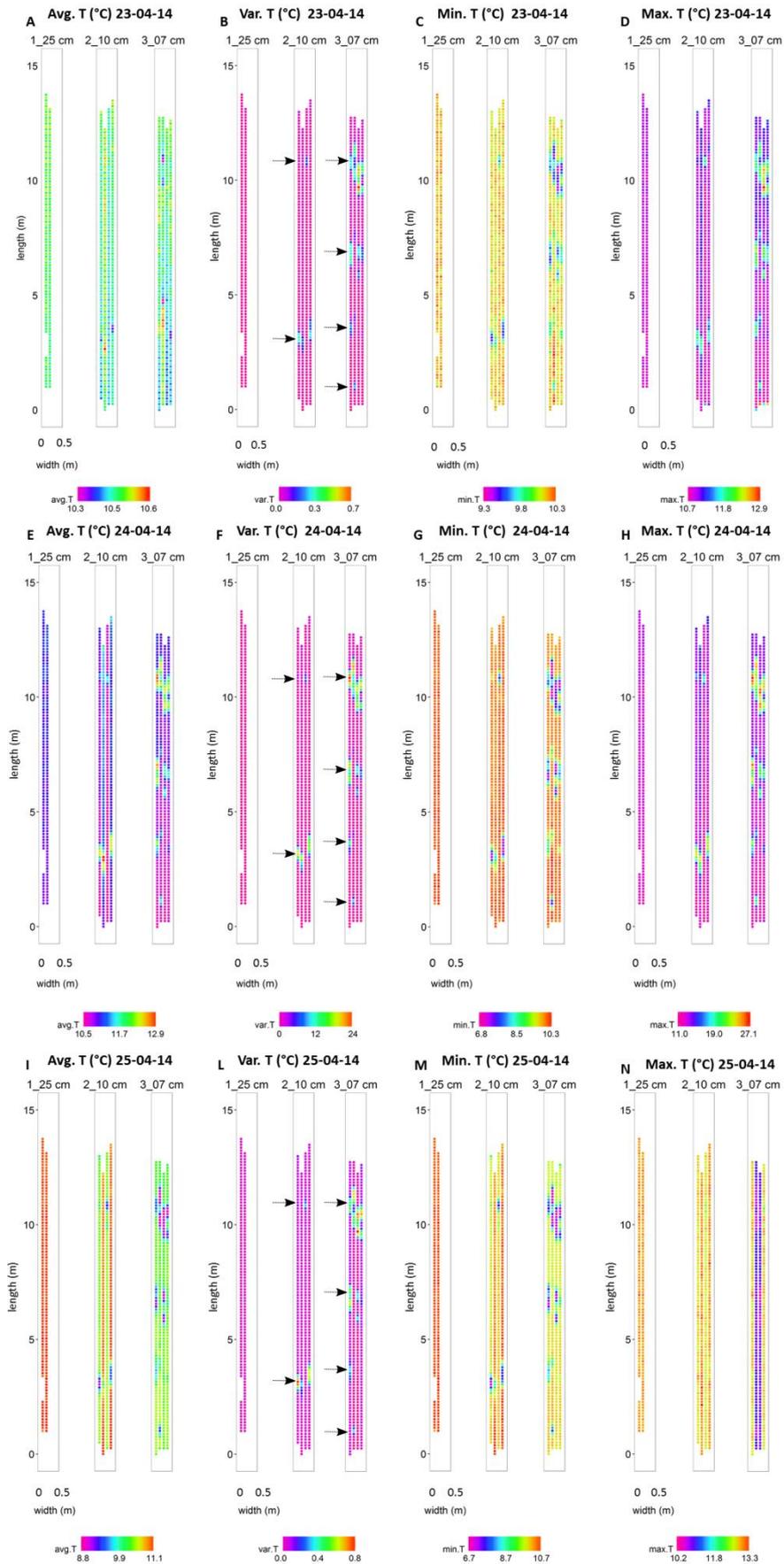


Figure 6. Average (A), variance (B), minimum (C) and maximum (D) spatial streambed temperature patterns distribution measured on 23-04-14; average (E), variance (F), minimum (G) and maximum (H) spatial streambed temperature patterns distribution measured on 24-4-14; average (I), variance (L), minimum (M) and maximum (N) spatial streambed temperature patterns measured on 25-4-14. Arrows on variance streambed temperature patterns distribution maps indicate the position of very shallow water or dry sediments spots in flume 2_10 and 3_07 cm where temperature variance was the highest.

The spatial correlations between streambed temperatures (daily average, variance, minimum and maximum for each DTS point along and across the flumes for each measurement day) and water depths (the corresponding water depth value of each DTS point in the flumes) varied between flumes and meteorological conditions (Table 6).

For flume 1_25 cm the relationship between streambed temperatures and water level was not as strong as that of the shallower flumes, and no substantial variability was observed between the different measurement days. In contrast, correlations between streambed temperatures and water level for the shallower flumes were generally stronger, significant and also more variable between day time and night time. Flume 3_07 cm, in particular, always exhibited the strongest spatial relationship in both directions, negative and positive, between streambed temperatures and water depths and the relationship was the strongest on 24-04-14. The results indicated that minimum streambed temperatures were positively correlated with water levels and the correlation was the strongest in the shallowest flume (0.44, 0.47 and 0.42 for 23-04-14, 24-04-14 and 25-04-14, respectively).

In contrast, maximum streambed temperatures were negatively correlated with water levels (except for 25-04-15 when measurements were stopped around 2 pm, probably before streambed temperatures peaked): the maximum streambed temperature correlations were always registered in the shallowest flume (-0.42, -0.43 and 0.29 for 23-04-14, 24-04-14 and 25-04-14, respectively). Correlation values for average streambed temperatures vs. water

depths appeared to be less strong and less variable among flumes and dates than those for maximum and minimum streambed temperatures.

Table 6. Spatial correlation analysis results for 23-04-14, 24-04-14, 25-04-14 obtained for the correlation of average, variance, minimum and maximum streambed temperatures in each flume vs. correspondent water level values (* $P < 0.001$; † no significant P -value).

Date	Flume	Avg. T	Var. T	Min. T	Max. T
23-04-14	1_25 cm	0.18†	0.20†	-0.13†	0.27†
	2_10 cm	0.07†	-0.35*	0.40*	-0.35*
	3_07 cm	0.03†	-0.39*	0.44*	-0.42*
24-04-14	1_25 cm	0.08†	0.18†	0.13†	0.10†
	2_10 cm	-0.35*	-0.34*	0.40*	-0.38*
	3_07 cm	-0.40*	-0.43*	0.47*	-0.43*
25-04-14	1_25 cm	-0.04†	0.02†	-0.08†	-0.27†
	2_10 cm	0.38*	-0.35*	0.39*	0.19†
	3_07 cm	0.40*	-0.37*	0.42*	0.29†

2.5 DISCUSSION

This research aimed to quantify potential drought impacts on the thermal regime of lowland gravel-bed rivers. Continuous observations of temperature differences between surface water inflow and outflow and spatial patterns of streambed temperatures in three outdoor flumes characterized by different water depths and co-evolved vegetation coverage over three days (23/25-04-14) revealed complex thermal variability. The interaction between different water depths along the characteristic pool-riffle-pool sequences and different vegetation coverage created water depth gradients along and across the three flumes with the formation of a variety of complex hydrologic habitats.

Net radiation is generally the main component of total energy flux in river systems (Caissie, 2006), accounting for 56 % of the total heat gain and for 49 % of heat loss in the River Exe, U.K. (Webb & Zhang, 1997). In the present study, solar radiation was the main flux

responsible for the daily outflow water temperature variations in the flumes (on average net radiation contributed for 64% to the total heat budget variations during the day and for 83% to the total heat loss during the night as simulated with our model). In addition, it has previously been acknowledged that the relationship between water and air temperature in a Devon river system is stronger and more sensitive for flows in the range below median discharge (Webb, Clack & Walling, 2003). Accordingly, in this study, the shallowest flume, 3_07 cm, representative of severe drought conditions, was especially responsive to fluctuations in solar radiation receipt and changes in air temperature. Using the high spatio-temporal capabilities of FO-DTS, it was possible to characterize the resulting high variability of thermal patterns in the flumes. Diverse meteorological conditions during the study period translated into different inter-flume streambed temperatures responses to radiation input, with flume 1_25 cm being the least responsive and the shallower flumes instead showing greater spatial and temporal temperature heterogeneity at the water-sediment interface. Similarly, surface outflow temperature variations were more pronounced in the shallower flumes, as shallower water bodies are characterized by reduced thermal capacity and greater water temperature fluctuations (Clark, Webb & Ladle, 1999).

The combination of multiple factors conducive to increased surface and streambed temperatures (e.g. shallow water depth, riffle sections directly exposed to the air, sparse vegetation coverage) present in flume 3_07 cm presumably accounted for its greater variability in surface water outflow and streambed water temperatures compared to the deeper flumes. Surface flow in 3_07 cm was distinguished by longitudinal discontinuities corresponding to the riffle sections characterized by bare dry sediments with braided flow patterns developing around the sparse macrophyte stands. The bare sediments, with substantially lower specific heat capacity than water (average heat capacity of primary

minerals $\approx 800 \text{ J Kg}^{-1} \text{ K}^{-1}$ vs. liquid water = $4184 \text{ J Kg}^{-1} \text{ K}^{-1}$; Berman & Brown, 1986) were exposed directly to solar radiation during daytime and were not sheltered from longwave radiation loss at night time, resulting in greater and quicker daytime warming compared to submerged areas, and faster night time cooling. A diel difference of $20.3 \text{ }^\circ\text{C}$ between the hottest ($27.1 \text{ }^\circ\text{C}$) and the coldest spot ($6.8 \text{ }^\circ\text{C}$) was registered for streambed temperatures for flume 3_07 cm on 24-04-14.

Special attention should be paid to maximum temperature as this is the most stressful for aquatic organisms, particularly under extreme meteorological conditions (e.g. droughts), when maximum values could be greater than their thermal tolerance threshold (Maazouzi *et al.*, 2011). As reported by Dixon *et al.* (2009), most ectothermic organisms, representing 99.9% of species on Earth (Atkinson & Sibly, 1997), possess a similar thermal window situated around $\sim 20 \text{ }^\circ\text{C}$, a range within which the organisms' development can occur. Ecological evidence, from the community to the individual level, showing a significant increase in the proportion of small-size species as a response mechanism to global warming (Daufresne *et al.*, 2009) and to drought conditions (Ledger *et al.*, 2011) has already been reported. In natural riverine ecosystems, obstacles (e.g. macrophytes aggregations) and streambed roughness (e.g. pool-riffle sequences) drive hydrological exchange processes between shallow groundwater and surface water through the hyporheic zone, due to discontinuities in slope and depth and changes in the direction of the flow (Brunke & Gonser, 1997). The direction of exchange processes varies with hydraulic head, whereas sediments permeability controls flow amount. The interactions between groundwater and surface water are characterized by a high temporal and spatial variability, due to seasonal fluctuations of surface water levels. Thus, the resulting ecological impacts on riverine ecosystems vary seasonally (Krause & Bronstert, 2007). Under typical summer conditions of low flow base flow mainly originates from groundwater, with

contributions up to 10% of the total river discharge (Krause & Bronstert, 2007). During hydrological stress conditions, these groundwater fluxes can act as an effective buffer against stream water warming because colder water is discharged to the stream when the stream most extreme temperatures are apt to occur (Poole & Berman, 2001). Hyporheic exchange promotes the formation of a mosaic of horizontal and vertical groundwater temperatures across the aquifer able to ameliorate particularly extreme stream maximum temperatures. Upwelling of colder groundwater into the main channel during low-flow conditions has ecological significance for biota, as it maintains minimum discharge able to support a diversified aquatic macrophytes community, it creates cold water refugia for stenotherms and for example it is essential for the survival of cold water fishes like salmonids (Ebersole, Liss & Frissell, 2003). Under future climate change with stream maximum temperatures likely exceeding actual values, it is evident how hyporheic flow becomes increasingly strategic and essential in supporting healthy aquatic communities.

Although changes in water depth likely explained a large proportion of the observed differences in surface and streambed temperatures between the three flumes, it was also probable that inter-flume variability in vegetation coverage accounted for the observed results. Shading is in fact well known to exert considerable influence on stream water temperature as it directly reduces radiative heat flux into the water (Sinokrot & Stefan, 1993; Bogan *et al.*, 2003). Previous studies have focused on the influence of riparian trees on stream temperatures, especially on maximum temperatures during summer months (Story, Moore & Macdonald, 2003; Johnson, 2004; Danehy *et al.*, 2005; Webb & Crisp, 2006; Hannah *et al.*, 2008a; Malcolm *et al.*, 2008; Garner *et al.*, 2014b, 2015b). However, this study is the first work exploring the combined effect of different water depths and co-evolved aquatic vegetation coverage on both surface and streambed temperature patterns at high spatial and

temporal resolution. When assessing the effect of shading on stream water, the type of vegetation (e.g. growth form and morphology) and its density is an important element to be considered (Löfstedt & Bengtsson, 2008). During a clear day in presence of large stand of submerged macrophytes in a shallow water body, Dale and Gillespie (1977b) found that little light energy reached the streambed. Temperatures were higher at the water surface and lower at the water-streambed interface, resulting in a steep vertical temperature gradient in the water column; with sparse vegetation, smaller differences between surface water and streambed developed. Similarly, Clark *et al.* (1999) recorded vertical temperature contrasts due to the isolation from the main flow of a thin surface layer by aquatic vegetation such as *Ranunculus* spp.; this layer was subjected to strong heating by the sun (up to 2.7 °C above surface temperature in non-vegetated water areas), whereas the flow below the floating vegetation was protected. Furthermore, the temperature near the bottom of shallow water bodies where no shadows were cast by macrophytes varied with incoming solar radiation and quick temperature fluctuations were observed when radiation changed (up to + 10 °C in 6 hours at 0.20 cm depth when average net radiation was ~ 500 W/m²; Dale & Gillespie, 1977a). In this study, streambed temperature extrema in flume 1_25 were generally lower than surface water values measured at the flume outlet. Streambed minimum temperatures were consistently lower than minimum surface water values throughout the duration of the experiment and maximum streambed temperatures were lower on 23-04-14 and 24-04-14. These findings are therefore likely due to the combination of deeper water and higher vegetation coverage relative to the other flumes, which increased the water body thermal capacity and buffered daytime atmospheric energy receipt, respectively. In contrast, this pattern was absent for the shallower flumes having greater exposed sediment:water surface ratios (leading to lower thermal buffering capacities) and more patchy shading by the sparser vegetation. In this

experiment, however, it was difficult to separate the single impacts of different vegetation coverage from different water depths on flumes thermal regimes, and rather the combined effects were observed. More research on the subject needs to be carried out to evaluate the influence of each factor.

In addition, shading by vegetation may also partially contribute to some of the temperature patterns observed in the flumes for streambed temperatures due to its ability to create differential heating between water within vegetation belts and open water. Lövstedt and Bengtsson (2008) suggested that vegetation belts can drive average temperature differences of up to 0.8 °C and an average reduction of net solar radiation within the vegetation up to 85%. Furthermore, in the daytime, shading reduces radiative inputs, decreasing warming over a given distance (Fullerton *et al.*, 2015), while, at night time, open water cools faster than shaded reaches, due to increased longwave and evaporative losses (Lövestedt & Bengtsson, 2008). These interacting processes may be therefore responsible in part for the high thermal heterogeneity generated in the flumes, especially in the shallower ones. For flume 3_07 cm, in particular, minimum streambed temperatures exhibited a faster and greater night-time cooling compared to the deeper flumes, with minimum streambed temperatures (6.7 °C) almost attaining minimum air temperature on 25-04-14 (6.9 °C). In contrast, in the deepest flume, the combined effect of the greater thermal capacity and the lower heat losses (potentially due to reduced evaporation in comparison to non-vegetated sections; Dale & Gillespie, 1976), prevented large daily temperature differences between minimum and maximum values. The more homogenous and dense vegetation coverage and the fact that all sediments were saturated translated into a less diversified spatial and temporal streambed temperature patterns distribution, with smaller differences between extreme temperature values both in space (along the flume) and in time (between day/night time and between different dates). Given the

reasonable degree of correlation between vegetation coverage and water depth (section 2.4.2) and water depth and streambed temperature metrics (section 2.4.4), this result supported the initial hypothesis that the combined effects of shallower water depth and sparser vegetation coverage would drive more marked temperature patterns in shallower flumes.

2.6 CONCLUSIONS AND IMPLICATIONS

Using the high spatio-temporal capabilities of FO-DTS, it was possible to detect high variability of thermal dynamics in co-evolved vegetated flumes with varying water depths. The results of this chapter indicate that variations in water depth, co-evolved aquatic vegetation coverage and morphologic features (pool-riffle-pool sequences) were major determinants in creating a complex spatial heterogeneity within the 15-m long and 0.5-m wide artificial channels. First, shallower water areas in the flumes, characterized by lower thermal capacity than the deeper areas, showed greater fluctuations in temperatures, with the exposed sediment features (riffle sections) distinctly showing the most extreme temperature values due to the lower heat capacity compared to the one of the water areas. Second, vegetation coverage likely also played a fundamental role via shading. Dense and continuous vegetation coverage, like that found in flume 1_25 cm, prohibited solar radiation from directly impacting the streambed sediments and reduced the evaporation rate from the flumes. Finally, water levels, together with vegetation, controlled the sensitivity of the flume temperature regimes to different meteorological conditions, particularly to changes in air temperature and solar radiation receipt. Given the expectation of more frequent and intense drought conditions under projected climate change, despite the use of artificial channels, these results highlight the importance of maintaining minimum water level conditions in lowland streams that are

able to host a stable aquatic vegetation community. Minimum water levels, together with the aquatic vegetation community, could promote the formation of complex thermal and hydrological habitats, able to better buffer the negative effects of extreme events such as heat waves.

More research is needed to distinguish water level contribution from vegetation coverage to stream thermal regimes and to better understand long term implications of water level fluctuations on stream thermal dynamics and, on a broader scale, on ecosystem functioning. There still remains uncertainty as to the extent of the impact of drought-induced terrestrialization occurring in lowland lotic ecosystems, and of its effects on river temperature regimes. Even though it is irrefutable that different growth forms possess different shading abilities, the consequences of increased numbers of riparian/invasive species replacing strictly aquatic plants (as projected under more severe future drought scenarios) to both surface and streambed temperatures is still unknown. Furthermore, extreme water temperatures during drought conditions which could exceed ectothermic organisms' upper limit thermal tolerance, stress the importance of the availability of both thermal and hydrological refugia (e.g. the hyporheic zone) to increase invertebrates and fish population resistance during drying events and resilience after the disturbance. The effects of water level fluctuations not only could imply different thermal dynamics in space and time but, on a long term, could alter ecosystem functioning and biodiversity as well, with riparian/invasive species replacing strictly aquatic plants, and with ectothermic organisms resistance/resilience threatened by the altered thermal regimes whether some effective protection processes for in-stream biota are not occurring (e.g. due to disrupted surface-groundwater linkages).

2.7 CHAPTER SUMMARY

Research in this chapter has examined the impacts of drought-induced water level fluctuations in lowland streams on patterns in surface water and streambed temperatures. Low flow drought conditions are in fact expected to become more frequent and more severe in the future due to the impacts of global environmental change. Findings suggest that variations in water level not only directly impact stream temperature, but also aquatic vegetation coverage which, in turn, contributes to affect stream temperature patterns and dynamics. Research in the following chapters further explores the implications of modifications in both the hydrological and thermal regime of streams due to climate change on streambed thermal heterogeneity, ecosystem resilience and functioning.

CHAPTER 3: AN EXPERIMENT TO
IDENTIFY THE CONTROLS OF
THERMAL STRESS IN STREAMBED
SEDIMENTS

3.1 INTRODUCTION

Due to anthropogenic stressors and climate change, the thermal and hydrological regimes of streams are expected to undergo drastic changes (Palmer *et al.*, 2009; van Vliet *et al.*, 2013; Kurylyk, MacQuarrie & Voss, 2014). Typical forecast alterations include changes in seasonal patterns of precipitations and runoff with more extended and severe drought conditions (Prudhomme *et al.*, 2014) and increase in water temperatures (Hari *et al.*, 2006; Webb & Nobilis, 2007; Mantua, Tohver & Hamlet, 2010; Kaushal *et al.*, 2010) due to the combined effects of greater atmospheric warming and reduction of streamflow, especially during warm, dry periods. In particular, during drought the reduced water flow causes the source of water for irrigation purposes to shift typically from surface to groundwater resources (Taylor *et al.*, 2013) with possible consequent groundwater depletion. This has important consequences on both the thermal and hydrological regimes of streams. In fact, lowered groundwater tables may disrupt upward-moving cool groundwater discharge to surface water during thermal stress (Tague *et al.*, 2008) causing loss of colder water microhabitats (e.g. thermal refugia *sensu* Ebersole *et al.*, 2003), and can result in upwelling flows shifting to downwelling flows (Stanley & Valett, 1992; Dahm *et al.*, 2003) exacerbating thermal impacts in the streambed; ultimately, the interactions between groundwater and surface water are not only altered but completely lost (Wada *et al.*, 2010; Kløve *et al.*, 2014).

The dominance of ectotherms in fresh waters (Durance & Ormerod, 2009; Woodward *et al.*, 2010b) means that climate change-induced modifications in water temperature have profound effects on aquatic organisms, from the community (Daufresne *et al.*, 2004; Woodward *et al.*, 2010b; Ledger *et al.*, 2012) to the individual level (Daufresne *et al.*, 2009; Ledger *et al.*, 2011). In thick, permeable, oxygenated and saturated streambeds where subsurface water

flows can mix with groundwater (e.g. hyporheic exchange flows), the hyporheic zone may offer more stable temperature conditions (Dole-Olivier, 2011), in other words a refuge that increases resilience to thermal stress. It is therefore of strategic importance for riverine biodiversity and ecosystem function and integrity to better understand how current and future modifications in the hydrological and thermal regimes of streams impact on streambed temperature patterns in order to preserve existing riverine thermal heterogeneity and to protect refuges (e.g. the hyporheic zone) from increased thermal stress.

In natural riverine systems, heat flows continuously between surface water, underlying sediments and groundwater (Constantz, 2008). Within the streambed, heat is transferred into and through the sediments as an outcome of four main processes: radiation, conduction, convection and advection, with advection being the pivotal heat-transfer mechanisms for investigating heat as a tracer of streambed water exchanges (Constantz, 2008). Heat advection is defined as the heat transfer occurring due to the movement of water through the streambed sediments, while conduction is the diffusive molecular transfer of heat between the streambed surface and underlying sediments along temperature gradients (Constantz, 2008). At downwelling sites a deep penetration of surface water temperature signal is expected (Norman & Cardenas, 2014) due to combined conductive and advective heat transfer. Shallower penetration of surface temperature signal is expected at upwelling locations due to upward inflow of groundwater that moderates temperatures (Norman & Cardenas, 2014). For example, advective fluxes induced by groundwater can have a remarkable effect on the thermal regime of small streams and of those where riparian vegetation becomes important (Caissie, 2006), although their significance can vary spatially and temporally (Story *et al.*, 2003).

Fibre-Optic Distributed Temperature Sensing (FO-DTS) allows continuous, high-resolution, temperature measurements at 0.25-1 m intervals along a fibre optic cable. A modified DTS application that consists in wrapping the fibre optical cable around a tube subsequently installed vertically in the streambed (Vogt *et al.*, 2010; Briggs *et al.*, 2012) converts the temperature profile along the cable into a depth profile (Vogt *et al.*, 2010) with a considerably increased spatial resolution. This improved DTS hyporheic application can be thus utilized to determine at high spatio-temporal resolution thermal stress into the streambed and to investigate how the direction of groundwater-surface water exchange impacts on the heat transfer.

Research examining the effects of combined altered thermal and hydrological regimes induced by climate change and their potential effects on freshwater biodiversity to date is still limited (Pyne & Poff, 2017), and the few existing studies have generally used a modelling approach to forecast the effects on species distribution (Wenger *et al.*, 2011; Ruesch *et al.*, 2012; Kuemmerlen *et al.*, 2015); studies focusing on how variations in stream temperature and hyporheic exchange flows (e.g. changes in streamflow between gaining and losing conditions) in unison influence streambed temperature dynamics are even rarer. To date, only Maazouzi *et al.* (2017) created in a stream section an artificial streambed drying to examine the vertical migration of invertebrates in the hyporheic zone; throughout a 2-day monitoring study the effects of drying on hydrological exchange patterns and hyporheic water temperatures changes at four depths were investigated as well. Despite the proportion of intermittent rivers is likely to increase with climate-induced loss of streamflow continuity over time becoming a common feature even for perennial rivers (Datry, Larned & Tockner, 2014b; Jaeger, Olden & Pelland, 2014), in the near future connectivity over space may be entirely sustained by refuges like perennial patches or pools, even though reduced in size and

isolated from each other. And because climate change will not only alter mean temperatures but also daily temperature ranges (Easterling *et al.*, 2000), and because short-term changes in thermal variance can have as much or more impact on organismal fitness as does the mean temperature (Bozinovic *et al.*, 2011), it is more and more crucial to monitor the amount of thermal stress in space and time before habitat temperatures reach and ultimately exceed organisms' thermal tolerance. Therefore, there is an increasing need to investigate streambed sediments temperature distributions at high spatio-temporal resolution in order to identify potential refuge habitat conditions for aquatic biota from increasing warming.

The aim of this study was to systematically analyse temperature distributions of up- and downwelling flows in gravel streambeds of laboratory mesocosms following increased surface water temperatures that simulated different thermal stress severity in isolated pools, to test potential refuge habitat conditions for ectothermic organisms under different hydrological exchange and warming scenarios. Two hypotheses were tested:

1. surface thermal stress penetrates to greater depths in the streambed under downwelling conditions, whereas cool water upwelling attenuates surface temperature signal at shallow depths under upwelling conditions; therefore, the direction of groundwater-surface water exchange plays a crucial role in moderating temperature extremes in the streambed sediments;
2. nevertheless, streambed sediments has the potential to serve as a thermal refuge for some river organisms to increased surface water temperatures during warming under both flow directions owing to the attenuation of surface heat with increasing depth.

3.2 METHODS

3.2.1 EXPERIMENTAL SET UP

A set of 10 experimental mesocosms was used to mimic gravel streambeds and simulate increased surface water temperatures and change in flow direction (Figure 7). 5 distinct temperature treatments were generated in the surface water, from 15 to 27 °C every 3 °C, and 2 contrasting hydrological conditions, with upwelling and downwelling flow. Fibre-Optic Distributed Temperature Sensing (FO-DTS) was deployed for high-resolution temperature monitoring of vertical temperature profiles. The experiment was conducted for 14 days, from 2016-04-18 to 2016-05-02. Throughout the experiment, mesocosms were kept in a temperature-controlled room ($16.7\pm 0.5^{\circ}\text{C}$).

3.2.2 MESOCOSMS DESCRIPTION

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). Each mesocosm was characterized by a 30-cm surface zone (10 cm at the top were left for gas exchange and 20 cm for surface water), and by a 90-cm sediment zone representing the streambed (Figure 7).

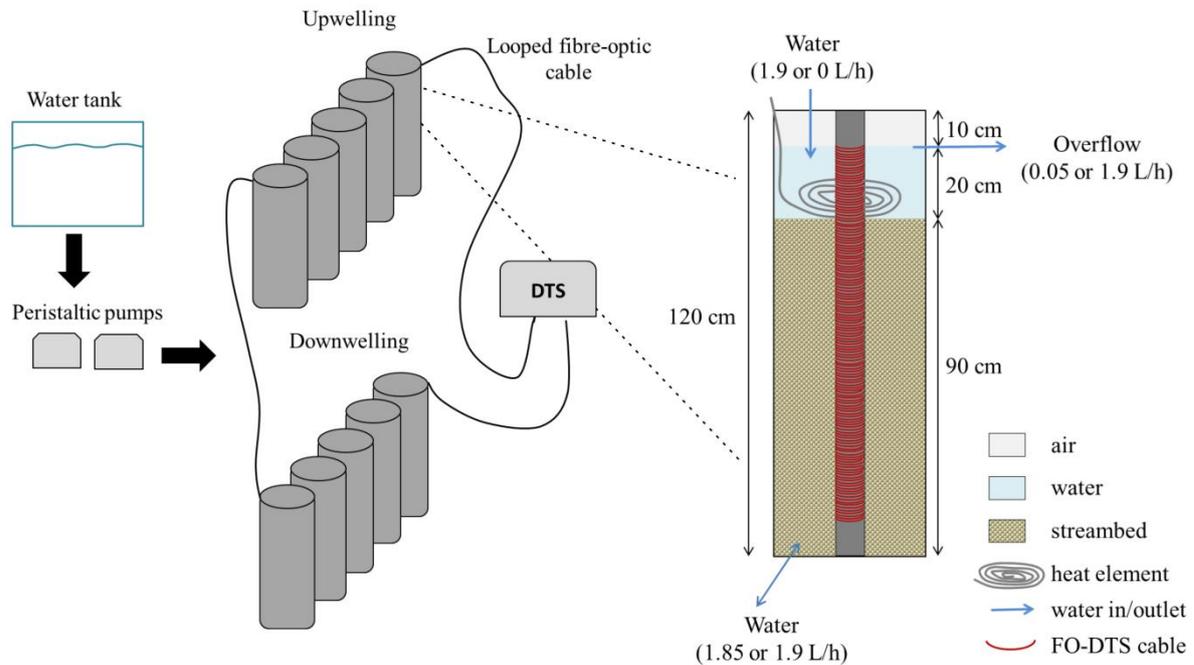


Figure 7. Experimental design with a schematic representation of mesocosms.

3.2.3 SURFACE WATER TEMPERATURE AND FLOW TREATMENTS

Surface water temperatures of 15, 18, 21, 24 and 27 °C were generated to simulate distinct warming of river water using heating cables (0.5 cm diameter) (Hydrokable, Hydor Inc. Sacramento, CA USA) placed onto the sediment surface and coiled around the inner wall of the mesocosms (Vander Vorste *et al.*, 2016a). An electronic thermostat (± 0.1 °C) (Hobby, Dohse Aquaristik GmbH & Co., Graftschaff, Germany) kept surface water temperatures constant throughout the experiment.

Up- and downwelling conditions were generated using peristaltic pumps (Figure 7). 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 tap water 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 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 streambed by pumping out interstitial water from the bottom (1.85 L/h), while 0.05 L/h drained through a 2-cm diameter hole, located 10 cm below the top of each mesocosm. Water volume in each mesocosm (22.8 L) was renewed for both flow paths every 12 hours.

3.2.4 HIGH-RESOLUTION TEMPERATURE SENSING MONITORING

Vertical temperature patterns in the mesocosms were monitored at high spatial and temporal resolution using 10 fibre-optic high resolution temperature sensors (HRTS) (Briggs *et al.*, 2012) specifically built for the purpose. Specifically, a small armoured bend-insensitive fibre-optic temperature sensing cable with stainless steel loose tube containing two 50- μm multimode optical fibres bedded in a gel, 1.6 mm diameter, shielded in a polyamide outer sheath (Brugg Kabel AG, Brugg, Switzerland) was wrapped around PVC pipes to create HRTS with 0.004 m vertical sampling resolution. The pipes (6-cm external diameter hollow PVC pipes, 1.2 m long) were pre-threaded at a specific pitch so that physical contact between consecutive coils was avoided. The threaded part was 1-m long, leaving the first and last 10 cm of the pipes unthreaded. The fibre-optic cable was wrapped around the pipes from top to bottom, leaving at least 5 m of cable at the top of each HRTS to allow in series connection to the next HRTS. Then, the cable was brought back to the top of the pipes by letting it pass through to a hole made at the bottom of each pipe. A Fujikura 19S Fusion Splicer was used to connect all HRTS in series, creating a continuous cable from the 10 HRTS (Briggs *et al.*, 2012). The two ends of the cable were attached through E2000 connectors to two respective channels of the DTS unit to create a continuous loop (Figure 7).

Each HRTS was placed vertically into the sediments, in the centre of the 10 mesocosms (Figure 7). The DTS instrument used for this application was a Silixa XT-DTS™ (Silixa Ltd.,

UK), having a sampling resolution of 25 cm and offering a spatial resolution of > 50 cm along the fibre based on the Nyquist criterion (van de Giesen *et al.*, 2012). 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 continuously performed to improve accuracy of the DTS system. Specifically, at both ends of the fibre-optic cable, sections of > 20 m were coiled and kept at a constant temperature in an iced water bath (Tyler *et al.*, 2009), mixed continuously by a bilge pump and their monitoring temperatures matched each time a measurement was taken to account for differential loss. As an input for the temperature offset calculation one of the two external temperature probes supplied with the DTS system was used by placing it in the same bath where the reference sections were kept.

3.2.5 DATA ANALYSIS

The temperature records at 0.004 m spatial and 2 min temporal resolution were averaged over 2-week time to produce for each HRTS a temperature profile showing mean thermal habitat conditions in the streambed throughout the experiment; in addition, temperature for each 2 min timestep averaged over 20-min was plotted by depth through time along each HRTS to explore at high spatio-temporal resolution patterns in the propagation of thermal stress with the flow direction. The *matrixStats* package (Bengtsson, 2015) in R (R Core Team, 2016) was used to calculate for each mesocosm the mean temperature profile and the associated standard deviation for the total duration of the experiment (Figure 8), and the 20-minute average streambed temperature profile (Figure 9). The *ggplot2* package (Wickham, 2009) was used to produce all plots. Paired t-tests were performed in R to find whether any significant difference

in the mean streambed temperatures between up- and downwelling flow conditions for each temperature treatment existed.

3.3 RESULTS

3.3.1 VARIATION IN STREAMBED TEMPERATURE DISTRIBUTIONS BETWEEN UP- AND DOWNWELLING FLOW UNDER WARMING

Temperature distributions into streambed sediments varied between up- and downwelling flow. Except for 15 °C temperature treatment, in all other cases heat generated in the surface water was propagated to a greater depth under downwelling than under upwelling flow (Figure 8) due to the combined conductive and advective heat transport. In contrast, under upwelling conditions, upward advection due to the inflow of constantly cooler water at the bottom of mesocosms (mean temperature throughout the experiment: 15.0 ± 0.2 °C) resulted in smaller variations in streambed temperatures.

Throughout the experiment, mean temperature in the streambed from the interface between free water-sediments to the bottom of HRTS ranged from 15.8 ± 0.3 °C (15 °C temperature treatment) to 16.3 ± 1.5 °C (27 °C temperature treatment), with a mean difference of 0.5 ± 1.1 °C between the warmest and the coldest temperature treatment under upwelling conditions. Under downwelling conditions, mean temperature in the streambed exhibited greater variability among temperature treatments, and ranged from 15.7 ± 0.2 °C (15 °C temperature treatment) to 20.6 ± 2.9 °C (27 °C temperature treatment), with a mean difference of 4.9 ± 2.0 °C between the warmest and the coldest temperature treatment. Mean temperature in the streambed under upwelling conditions was indeed 1.2, 2.3, 3.2 and 4.3 lower for 18, 21, 24

and 27 °C temperature treatments than downwelling flow treatments, respectively (t-test, $P < 0.0001$). For 15 °C temperature treatment, mean streambed temperature was 0.1 °C lower under downwelling flow instead (t-test, $P = 0.009$).

At a depth of 0.10 m in the streambed mean temperature for all temperature treatments under upwelling conditions was below 20 °C that is a lower temperature than the mean upper thermal tolerance for the most sensitive freshwater invertebrates (21 °C , Stewart *et al.*, 2013), whereas much greater depth needed to be descended to find the same mean temperature under downwelling conditions. While streambed sediment under downwelling flow for 15 and 18 °C temperature treatments always exhibited a mean temperature below 20 °C at all depths, the same mean temperature was found on average at a depth of 0.15, 0.33 and 0.43 m for 21, 24 and 27 °C temperature treatment, respectively. For 27 °C treatment temperature in particular, this result implied that almost half of the entire streambed at disposal, 0.43 out of 0.90 cm, was not suitable to host and give refuge to ectothermic organisms from surface warming.

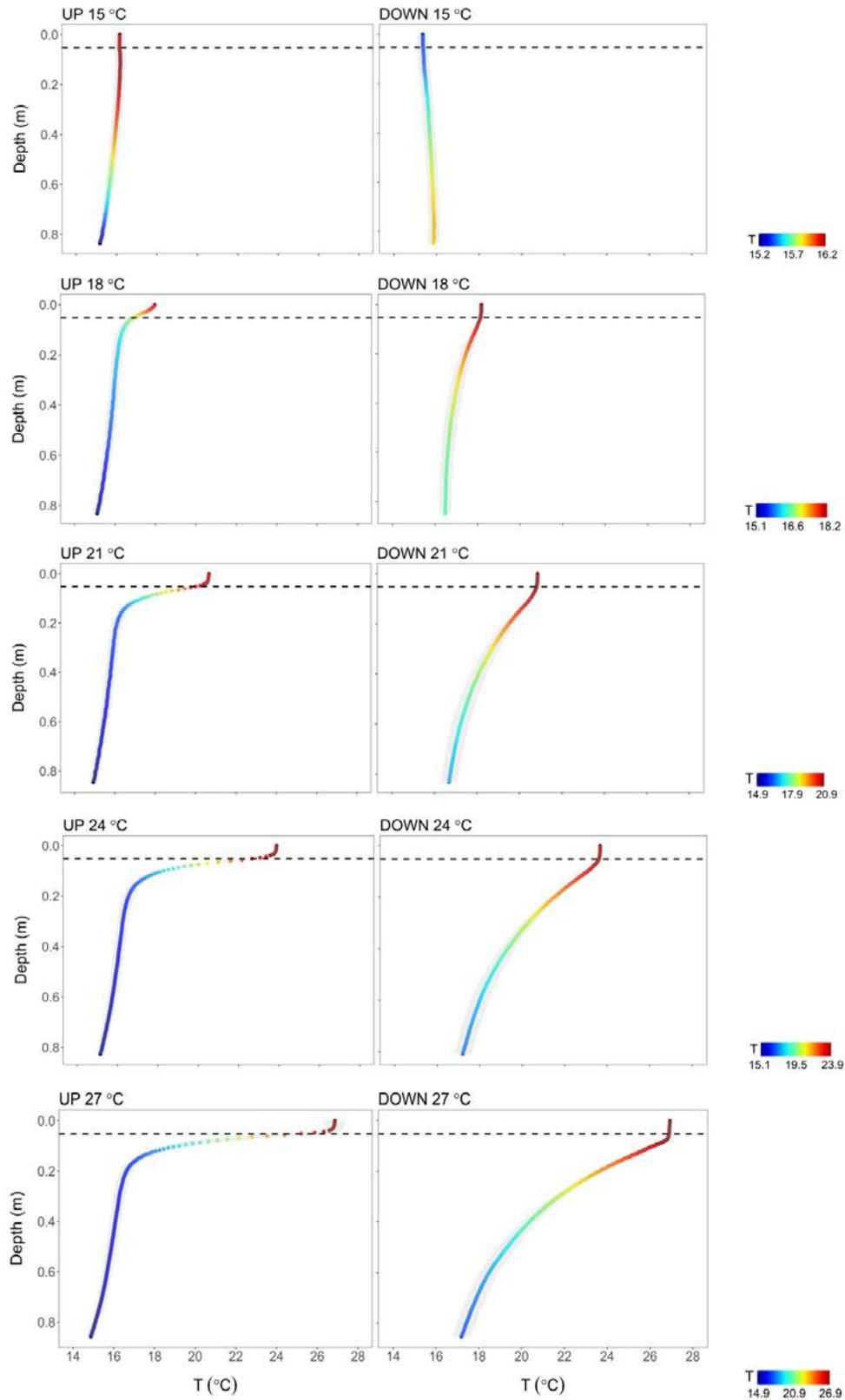


Figure 8. Streambed temperature profiles throughout the experiment for each temperature and flow treatment with relative standard deviation (in grey). The dashed line represents the interface between surface water-streambed sediments (due to homogeneous thermal conditions only 5 out of 20 cm for surface water are depicted).

Furthermore, the analysis of 20-min average streambed temperature profiles (Figure 9) revealed more clearly that the direction of hydrologic exchange flow impacted not only on mean streambed temperatures, but also on temperature extremes (e.g. minimum and maximum values at 20-min intervals). In particular, downwelling flow always showed greater values for both minimum and maximum streambed temperatures for all temperature treatments (Table 7), except for 15 °C where the lower temperature limit was greater for upwelling conditions. This implied that broader range of temperatures were found for each temperature treatment (except for 15 °C) under downwelling than upwelling conditions.

Diel temperature cycles are visible in Figure 9 due to small temperature variations between day and night hours in the room temperature (≤ 0.5 °C) that could not be removed while the experiment was running.

Table 7. Mean (\pm SD) and range (min-max) for streambed temperatures (°C) for each temperature and flow treatment obtained from the 20-min average streambed temperature profiles.

T treatment	Flow treatment	Mean T (°C)	Range T (°C)
15 °C	UP	15.8 \pm 0.4	2.0 (14.7 – 16.7)
	DOWN	15.7 \pm 0.3	1.7 (14.8 – 16.5)
18 °C	UP	15.8 \pm 0.4	2.7 (14.6 – 17.3)
	DOWN	17.0 \pm 0.6	3.4 (15.0 – 18.4)
21 °C	UP	15.9 \pm 0.8	5.8 (14.4 – 20.2)
	DOWN	18.2 \pm 1.3	6.3 (14.7 – 21.0)
24 °C	UP	16.3 \pm 1.1	8.2 (14.7 – 22.9)
	DOWN	19.5 \pm 1.9	8.9 (14.8 – 23.7)
27 °C	UP	16.3 \pm 1.6	12.5 (14.5 – 27.0)
	DOWN	20.6 \pm 2.9	12.6 (14.9 – 27.5)

However, even though varying in size, streambed sediments could provide for all temperature treatments a potential thermal refuge for surface organisms under both flow conditions, with the highest temperature warming scenario under downwelling flow (27 °C) representing the

most extreme case under which organisms would need to be able to burrow at least as deep as 0.43 m in the streambed to find relief from thermal stress.

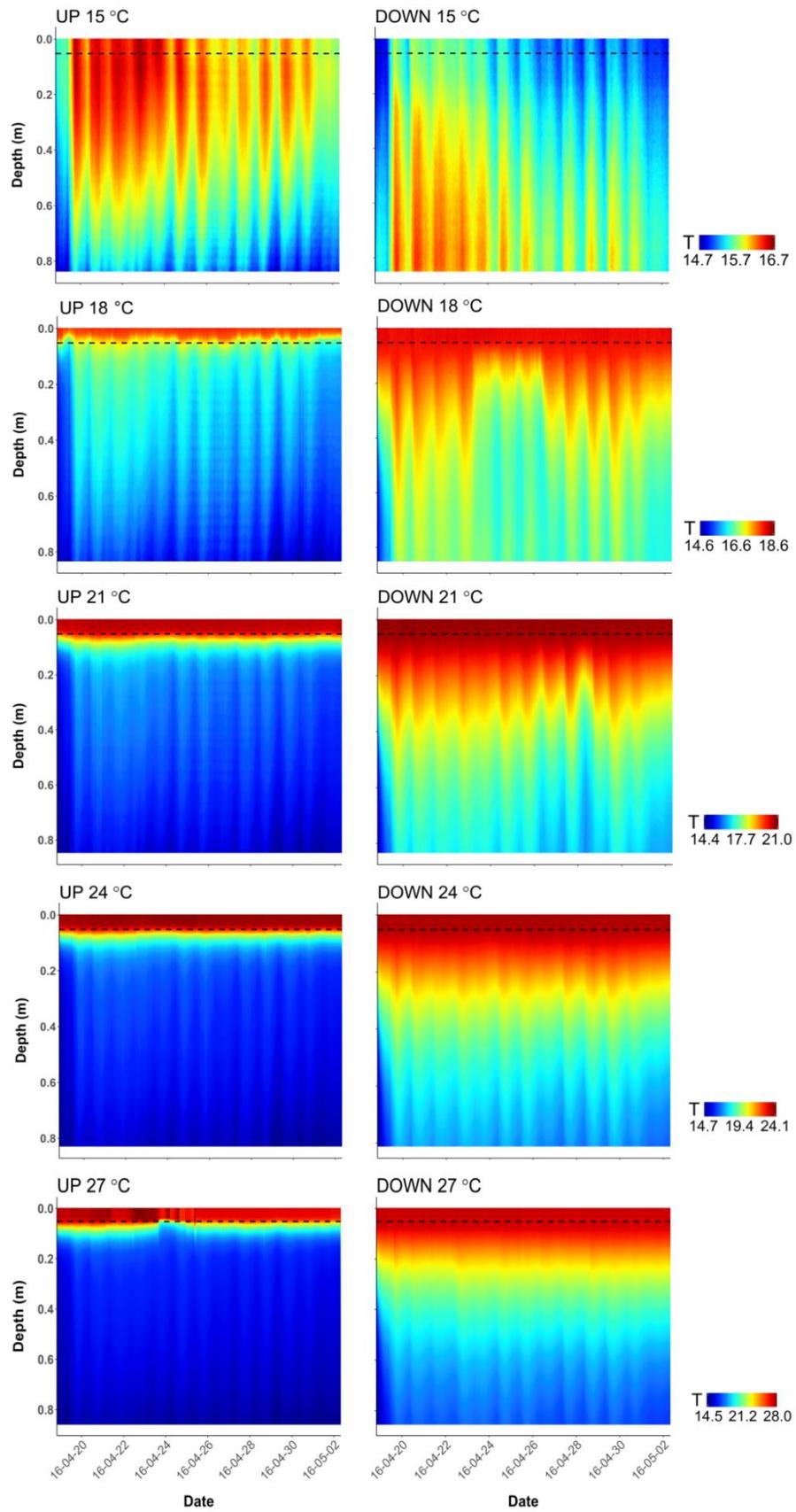


Figure 9. 20-min average streambed temperature profiles for each temperature and flow treatment.

3.4 DISCUSSION

Climate warming together with direct human modification through stresses such as water abstraction and flow regulation threaten stream ecosystems, undermining their functioning (Woodward *et al.*, 2010b; Pyne & Poff, 2017; White *et al.*, 2017). During warming, base flow is mainly maintained by deeper groundwater only; yet, declining groundwater levels alter the direction of flows between surface and ground waters (Dahm *et al.*, 2003), and this in turns modifies streambed thermal regime as heat is carried into the streambed with downwelling surface water.

The findings of this study demonstrate that the direction of groundwater-surface water exchange impacts on the transfer of thermal stress into gravel streambeds under different warming scenarios. Expect for 15 °C, mean temperatures in the streambed was lower under up- than downwelling flow for all other temperature treatments tested, indicating that during warming streambed sediments provided a more efficient potential thermal refuge under upwelling flow. In fact, the constant upward inflow of cooler water buffered thermal stress and even for the warmest temperature treatment (27 °C) only little thermal variation in the mean streambed temperature was produced compared to lower temperature treatments. Not only mean temperatures but also temperature extremes were attenuated under upwelling conditions, reducing temperature ranges in the streambed sediments. Similar results reporting drought impacts being buffered by high groundwater levels were found in previous studies (Clark *et al.*, 1999; Wood & Petts, 1999). In contrast, heat was propagated to greater depth under downwelling flow due to combined conductive and advective heat transport, reducing the extent of streambed habitat where thermal conditions were suitable for hosting aquatic biota. Specially for 27 °C temperature treatment, the size of streambed where thermal

conditions were below the upper thermal tolerance of 21 °C for sensitive freshwater insect taxa was highly contracted to deep sediments only, suggesting that severe warming can have remarkable effects on the thermal regimes of streams in areas dominated by downwelling. Indeed, elevated water temperatures in both benthic and hyporheic habitats combined with changes in up- and downwelling water in a chalk stream in the UK during a severe drought triggered benthic organisms to migrate into the hyporheic zone and to utilize the shallow hyporheic sediments as a refuge (Wood *et al.*, 2010). While the transition to high and low temperatures was sharp under upwelling flow and within 0.10 m depth surface thermal stress was highly buffered for all temperature treatments, in contrast distinct streambed temperature gradients were observed under downwelling flow (temperature decreasing with depth). Although limited to the deeper sediments for the higher temperature treatments under downwelling flow, these results indicate that gravel streambeds of isolated pools can provide potential thermal refuge from increased surface warming when vertical hydrological connectivity is maintained, enhancing the resilience of freshwater organisms to warming.

Throughout the experiment, simulated up- and downwelling flows were promoted by sediment homogeneity (clean, medium-size gravel with no fines present to fill gaps), with constant and equal flux along the mesocosms (1.9 L/h); as such, the resulting interstitial water velocity (22.3 cm/h) favoured on one hand the heat transport into deep sediments under downwelling flow, on the other thermal stress was highly buffered in the shallow sediments under upwelling conditions. These hydrological and physical conditions are rarely met in natural riverine systems, as river beds are rarely uniform (Evans *et al.*, 1998). More realistically, the heterogeneous arrangement of channel features and of areas of different grain sizes and sediment hydraulic conductivity normally produces a mosaic of exchange flow patches (Boulton *et al.*, 2010), and, at a larger spatial scale, local flowpaths can be nested in a

major upwelling/downwelling (Maazouzi *et al.*, 2017). In particular, hydraulic conductivity is one of the most important factors influencing hydrological exchange rate and its depth (Boulton *et al.*, 2010; Menichino & Hester, 2014), and it is known to vary in both space and time (Storey *et al.*, 2003; Genereux *et al.*, 2008; Stewardson *et al.*, 2016). Furthermore, hydraulic conductivity controls the relative importance of heat advection vs. conduction (Menichino & Hester, 2014): it has been found that heat advection increases with increasing hydraulic conductivity, and its influence is particularly important in gravel streambed (Cardenas & Wilson, 2007a). Therefore, different patterns of the observed temperature distributions might have been found by changing sediment streambed properties (e.g. sand instead of gravel) and flow rates in the mesocosms. Although conditions created in the mesocosms were simplified (e.g. distinct up- and downwelling flows in homogeneous streambed), the findings of this study and the high-resolution temperature monitoring method employed shed light on the potential functional significance of streambed sediments under up- and downwelling conditions in a warming world. Protecting streambed thermal heterogeneity from increased thermal stress by recovering surface-groundwater hydrological linkages should be a priority for river and water managers.

3.6 CONCLUSIONS

To summarize, this study identified the primary drivers of thermal stress into streambed sediments. The direction of groundwater-surface water exchange impacted on the transfer of thermal stress into gravel streambeds under all warming scenarios tested. Surface water signal was highly attenuated at shallow depths under upwelling conditions for all temperature treatments owing to upward advection of cooler water; on the contrary, streambed sediments

under downwelling conditions provided a potential less efficient thermal refuge capacity, due to combined conductive-advective downward heat transport up to considerable depths in the sediments. However, within the range of surface water temperatures tested (15-27 °C) and the interstitial water velocity used (22.3 cm/h), deep sediments (e.g. > 0.43 m depth in the case of 27 °C temperature treatment under downwelling conditions) under both flow directions provided a potential thermal refuge to benthic organisms during warming as temperatures were below the upper thermal tolerance of the most sensitive freshwater insect taxa (21 °C). However, other factors like sediment homogeneity and sediment hydraulic conductivity could have contributed to observed temperatures distributions of up- and downwelling flows in the mesocosms. The use of laboratory mesocosms, although with simplified conditions compared to real world, was useful to explore and test mechanisms of thermal stress transfer in streambed sediments under different warming scenarios.

3.7 SUMMARY

Research in this chapter has used high resolution FO-DTS monitoring technology to characterize streambed sediments temperature distributions of up- and downwelling flows in artificial laboratory mesocosms under different warming scenarios. The primary drivers of thermal stress in streambed sediments were identified, and potential implications for benthic organisms discussed. Findings, in accordance with previous studies (Dole-Olivier, 2011), suggest that the direction of water exchanges is indeed an important factor controlling the refuge capacity of hyporheic sediments, and subsequently, extreme surface thermal conditions may reduce this capacity. This is further explored in Chapter 4.

CHAPTER 4: MESOCOSM
EXPERIMENTS REVEAL THE
DIRECTION OF GROUNDWATER-
SURFACE WATER EXCHANGE ALTERS
THE HYPORHEIC REFUGE CAPACITY
UNDER WARMING SCENARIOS

4.1 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 *et al.*, 2010b; 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 *et al.*, 2012) and altered food webs interactions (Woodward *et al.*, 2010a; 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, 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.*, 2014a; 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 *et al.*, 2011b), 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, 2008b; Krause, Hannah & Blume, 2011a), 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 &

Gonser, 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 *et al.*, 2011a). 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 *et al.*, 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 *et al.*, 2011a), 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 & Befly, 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. To address the above research gaps, this paper explores the combined effects of five different increased surface water temperature treatments and the direction of water exchange on the ability of *Gammarus pulex* (Crustacea: Amphipoda: Gammaridae) to migrate into the HZ as a response to warming. The primary aim of this study is to improve understanding of 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, real ranges of increased surface water temperatures, representing for instance disconnected standing pools associated with stream channel contraction, are simulated, and the direction of water exchange is manipulated. Specifically, the following hypotheses are tested:

1. The HZ provides a thermal refuge for river organisms when surface water temperature increases because it remains 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 is lower in downwelling conditions than in upwelling conditions because warmer surface water flow into the HZ raises the temperature of the HZ under downwelling conditions, but upwelling water remains cooler than surface waters.

4.2 METHODS

4.2.1 EXPERIMENTAL DESIGN

The study was carried out in laboratory conditions, by deploying a set of 10 experimental mesocosms to mimic gravel-bed river HZs and simulate increased surface water temperature and reversed flow direction due to climate change. 5 temperature treatments, from 15 to 27 °C, and 2 contrasting hydrological conditions, comprising upwelling (exfiltration) and downwelling (infiltration) flow (Table 8) were applied, and the vertical migration of *G. pulex* in response to these treatments was observed. This amphipod was used as a model organism (see details below).

High-resolution monitoring of vertical temperature profiles was possible by using Fibre-Optic Distributed Temperature Sensing (FO-DTS) and dissolved oxygen levels were kept close to saturation to avoid any possible anoxia. Rates of *Alnus glutinosa* leaf litter breakdown were used to assess the vertical migration of *G. pulex* into the HZ (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).

Table 8. 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.

Treatment	N^o of levels	Labels
Flow direction	2	UP DOWN
Surface water temperature	5	15 °C 18 °C 21 °C 24 °C 27 °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

4.2.2 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 (Figure 10 a,b,c). Each mesocosm was divided into two main parts (Figure 10 c); 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.

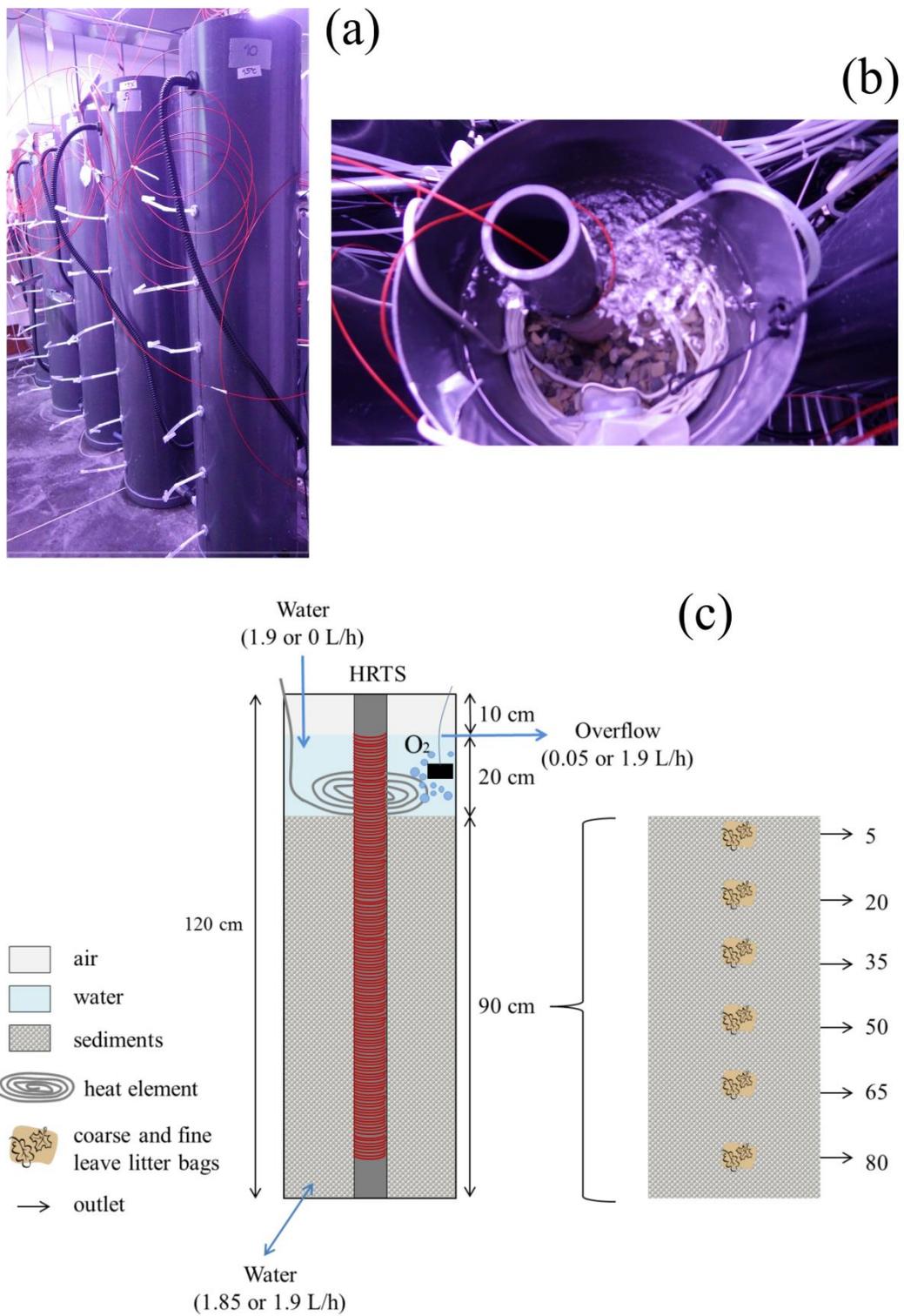


Figure 10. Mesocosm design with outside view (a), details from the inside (b) and mesocosm schematic representation indicating the dimensions of the surface and HZ, with the infiltration rates for down- and upwelling flow direction and the position of the fine and coarse leaf litter bags in the hyporheic sediments (c).

4.2.3 TEMPERATURE TREATMENTS

Five distinct surface water temperatures of 15, 18, 21, 24 and 27 °C were generated as outlined in Chapter 3 to simulate climate-induced warming of rivers water (Table 9). 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 *et al.*, 2010; van Vliet *et al.*, 2013). 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, mesocosms were kept in a temperature-controlled room (16.4 ± 0.4 °C).

Table 9. Mean value (\pm 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.

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

4.2.4 HYDROLOGICAL TREATMENTS

Up- and downwelling conditions were generated using peristaltic pumps. Detailed methods for this procedure are outlined in Chapters 3.

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. Dissolved oxygen and

temperature in interstitial water were measured 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 (Figure 10 a) 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.

4.2.5 HIGH RESOLUTION TEMPERATURE SENSING PROFILES

Vertical temperature profiles in the mesocosms for each of the 15-day experimental runs were continuously monitored at high spatial and temporal resolution using 10 high-resolution temperature sensors (HRTS) (Briggs *et al.*, 2012), specifically constructed for the purpose. Refer to Chapter 3 for a detailed description of this technique.

The number of HRTS that could be connected in series by splicing the fibre 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), the number of mesocosms was limited to 10 and the experiment repeated three times using an identical design.

4.2.6 MODEL ORGANISM

G. pulex (Amphipoda: Crustacea, Linnaeus, 1758) was used 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, adult amphipods of similar size (5-7 mm) were collected twice (early March and mid-May 2016) from a first-order stream near Dijon, France (see Vander Vorste *et al.*, 2016a b for details). The amphipods were kept in a temperature-controlled room (16.4 ± 0.4 °C) to acclimatize to temperature, water (collected from the same stream as amphipods, pH = 6.99, T = 10.4 °C, EC = 527 $\mu\text{s}/\text{cm}$) 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, Ravenna, Italy) kept water temperature constant (16.4 ± 0.4 °C) and air bubblers kept dissolved oxygen concentration near saturation. The amphipods were fed 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, 120 *G. pulex* were introduced into each mesocosm (3849 individuals/m³), 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.

4.2.7 ASSESSING *G. PULEX* SURVIVAL RATE

The percentage of individuals alive after 15 days was quantified 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.

4.2.8 ASSESSING *G. PULEX* VERTICAL MIGRATION

For each mesocosm, the average depth to which *G. pulex* migrated was assessed by determining (*G. pulex* mediated) leaf litter breakdown rates at different depths in the HZ (Figure 10 c, Table 8). 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 (Figure 10 c). The mesh size allowed amphipods to enter the bags freely and consume leaf litter. To facilitate colonization by fungi and increase leaf palatability (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 μ m, 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 °C for 24 h and weighed. At each depth, the net leaf litter breakdown (net LLB) rate was calculated 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).

4.2.9 STATISTICAL ANALYSIS

4.2.9.1 TEMPERATURE VERTICAL PATTERNS IN THE HZ FOR DOWN- AND UPWELLING CONDITIONS

To test the first hypothesis that the HZ provides a thermal refuge for *G. pulex* when surface water temperature increases, the vertical temperature profiles for each treatment were first explored. Secondly, to evaluate whether flow direction and surface water temperature influenced differences in HZ temperature between depth 1 and depth 6 (hereafter ΔT), linear mixed effect models with Gaussian error distribution (LME) were used (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.

4.2.9.2 SURVIVAL RATES AND VERTICAL MIGRATION OF *G. PULEX*

To test the second hypothesis that flow direction can impair the capacity of the HZ to provide a refuge when surface water temperature increases, a LME was used to test differences in *G. pulex* survival rates among temperature and flow direction treatments. 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, differences in vertical migrations of *G. pulex* among treatments were tested. To do so, a leaf litter breakdown averaged depth (D) for each mesocosm was first calculated, as follows:

$$D = \sum_1^6 (\text{net LLB} * \text{depth}) / \sum_1^6 \text{net LLB}$$

D represents the average depth (m) at which *G. pulex* mediated leaf litter breakdown (LLB) was the highest. A LME was then fit to test 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. The percentage of *G. pulex* found in each mesocosm was included in the model 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).

4.3 RESULTS

4.3.1 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) (Figure 11). On average,

temperature at depth 3 was below 20 °C and ranged from $15.9 \pm 0.1^\circ\text{C}$ (18 °C, upwelling treatment) to $19.6 \pm 1.2^\circ\text{C}$ (27 °C, downwelling treatment).

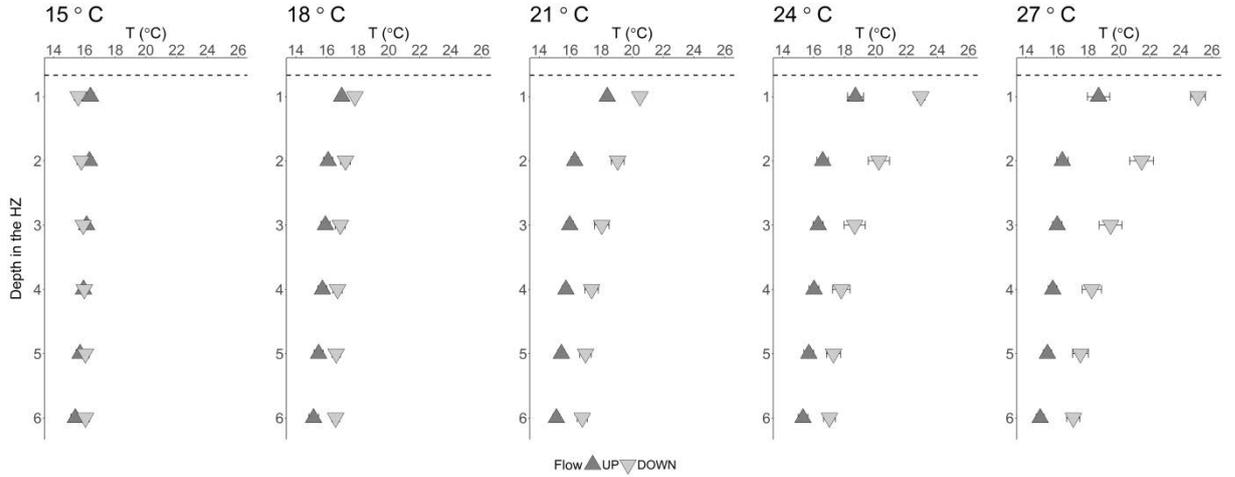


Figure 11. Mean temperature values with standard deviation ($n = 3$) in the HZ for both up-and downwelling flow treatments at increasing surface water temperature. Dashed horizontal line represents location of the free water-sediment interface.

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 10, interaction factor, $P < 0.0001$).

Table 10. 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
ΔT	Flow direction (Flow)	1	14.75	0.1465
	Mean surface water T measured (T)	1	285.16	< 0.0001
	Flow x T	1	49.69346	< 0.0001

When surface water temperature increased, ΔT increased more under downwelling ($R^2 = 0.98$) than upwelling ($R^2 = 0.60$) conditions (Figure 12). 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.

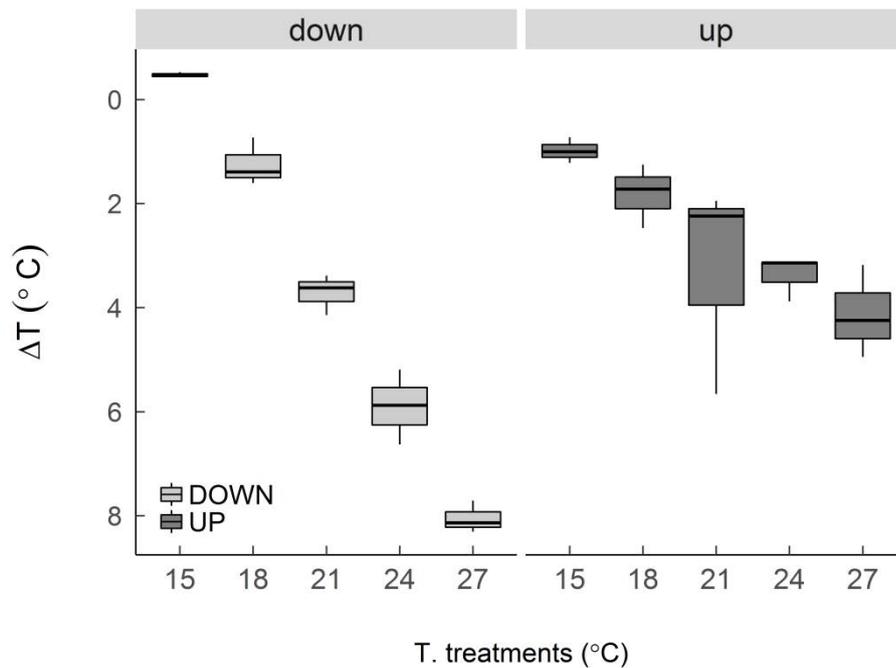


Figure 12. Median of the temperature differences (\pm SD) between deep and shallow hyporheic sediments (ΔT , °C) for both down-and upwelling flow conditions at increasing surface water temperature.

4.3.2 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 (Figure 13, Table 11). On average, 64 ± 11 % of amphipods survived under downwelling conditions, whereas 44 ± 10 % survived under upwelling conditions (Figure 13).

Table 11. 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.

Dependent variable	Factor	d.f.	F-value	P-value
% <i>G. pulex</i> found alive	Flow direction (Flow)	1	131.88	< 0.0001
	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	< 0.0001
	Mean surface water T measured (T)	1	7.67	0.0118
	% <i>G. pulex</i> found	1	0.03	0.8663
	Flow x T	1	1.77	0.1988
	Flow x % <i>G. pulex</i> found	1	0.16	0.6950
	T x % <i>G. pulex</i> found	1	0.46	0.5052
	Flow x T x % <i>G. pulex</i> found	1	0.05	0.8280

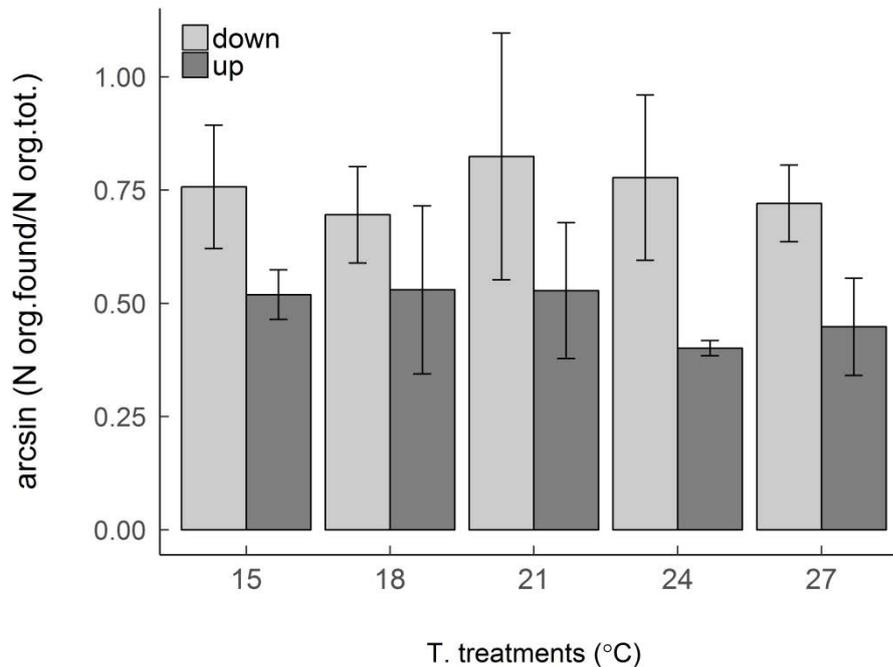


Figure 13. Mean (\pm SD) percentage of *G. pulex* found alive (arcsin-transformed) for each surface water temperature and flow direction treatments.

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 12). The mean percentage of *G. pulex* not found, presumably consumed by conspecifics (due to *G. pulex* propensity for cannibalism), was 43 ± 15 % (Table 12).

Table 12. Mean (\pm SD) percentage of *G. pulex* found with distinction between alive and dead organisms and mean (\pm SD) percentage of organisms not found for each temperature and flow direction treatment.

Surface water T. ($^{\circ}$ C)	Flow direction	% <i>G. pulex</i> found (n = 3)		% <i>G. pulex</i> not found (mean \pm SD, n = 3)
		Alive (mean \pm SD)	Dead (mean \pm SD)	
15	UP	46 \pm 5	3 \pm 1	50 \pm 10
15	DOWN	62 \pm 13	6 \pm 4	32 \pm 5
18	UP	47 \pm 15	3 \pm 2	50 \pm 15
18	DOWN	60 \pm 8	4 \pm 3	36 \pm 8
21	UP	48 \pm 14	2 \pm 2	50 \pm 17
21	DOWN	69 \pm 17	2 \pm 1	29 \pm 13
24	UP	38 \pm 3	2 \pm 1	61 \pm 14
24	DOWN	67 \pm 16	3 \pm 3	31 \pm 2
27	UP	41 \pm 9	3 \pm 2	57 \pm 10
27	DOWN	63 \pm 8	3 \pm 1	34 \pm 6

D, (leaf litter breakdown averaged depth), increased with surface water temperature (Table 11, $P = 0.012$) and varied with flow direction ($P < 0.0001$), with no significant interaction (Figure 14, Table 11). In upwelling conditions, D ranged from 0.13 ± 0.1 (15 $^{\circ}$ C treatment) to 0.22 ± 0.05 m (27 $^{\circ}$ C treatment), with a mean value of 0.18 ± 0.1 m. In downwelling conditions, D ranged from 0.27 ± 0.0 (15 $^{\circ}$ C treatment) to 0.49 ± 0.1 cm (27 $^{\circ}$ C treatment), with a mean value of 0.37 ± 0.1 m.

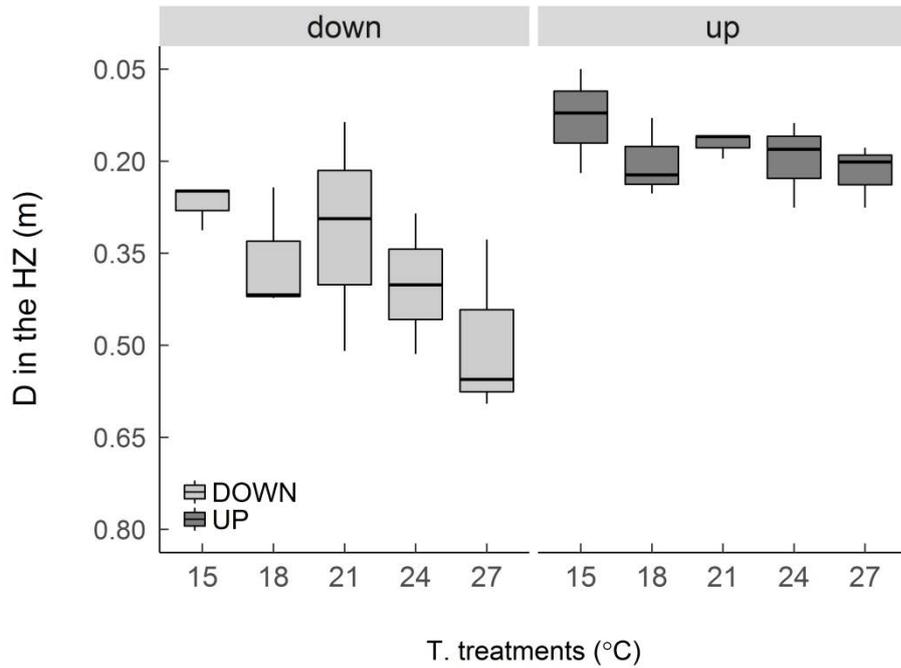


Figure 14. Median of the leaf litter breakdown averaged depths (m) for both down-and upwelling flow conditions at increasing surface water temperature.

4.4 DISCUSSION

Vulnerability of aquatic organisms to global warming has been demonstrated (Verberk *et al.*, 2013; Pyne & Poff, 2017), particularly for those species occupying habitats near the limits of their thermal tolerance (e.g. in arid regions Stewart *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, the findings of this study show that hyporheic sediments could be a potential refuge for *G. pulex*. Specifically, 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, the hypothesis that downwelling flow areas

provide less effective refuges compared to upwelling zones is not supported. These results challenge the current paradigm that upwelling areas provide better refuges for river invertebrates during disturbance. Although the response of only one species is tested, the results suggest 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.

4.4.1 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 *et al.*, 1999; Arrigoni *et al.*, 2008; Constantz, 2008; Krause *et al.*, 2011a). In this study, 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 the 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 *et al.*, 2011a), 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 *et al.*, 2013a).

4.4.2 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 the mesocosms, the created physical conditions were optimal 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 the study 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.

4.4.3 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; missing amphipods were assumed to be 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 *et al.*, 2013b) 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.

4.5 CONCLUSIONS AND IMPLICATIONS

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. The results of this study 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.

4.6 CHAPTER SUMMARY

In this chapter a complex experimental approach was adopted to test the hyporheic refuge hypotheses under different warming scenarios; in particular, the effect of alterations of the direction of groundwater-surface water exchange on the capacity of the HZ to provide a refuge for benthic invertebrates under warming was examined. Results indicated that at increasing surface water temperature leaf-litter breakdown was observed at a greater depth in the sediments under downwelling flow conditions, that is, *G. pulex* migrated deeper into the HZ compared to upwelling conditions, resulting in greater survival rates. However, under both up- and downwelling conditions, the study found evidence for potential use of the hyporheic zone as a thermal refuge under warming, as temperatures deep in the hyporheic zone never exceeded critical thermal thresholds for *G. pulex*. Hydroclimatological controls on

streambed sediments thermal dynamics are explored further in a real stream reach in Chapter 5.

CHAPTER 5: HIGH-RESOLUTION
SEASONAL VARIATIONS OF
STREAMBED TEMPERATURES OF A
FORESTED STREAM

5.1 INTRODUCTION

Streambed temperatures are highly dynamic both temporally and spatially due to complex exchange flows between the main channel and waters located vertically within the streambed, and laterally within alluvial sediments beneath the banks (e.g. hyporheic exchange flows, HEFs). These bi-directional subsurface hydrologic exchange flows, in which flowing surface water is temporally and repeatedly conveyed through the subsurface and returned to the stream (Harvey & Bencala, 1993), are activated by heads gradients created by topographic features of the river bed (Wondzell, 2006; Hester & Doyle, 2008). The presence of channel-spanning geomorphic features like logs, steps and riffles and particularly during base flow conditions when features are emergent, contributes in fact to flow roughness by causing a variation in local water-surface slope, thus increasing the force to drive subsurface flow (Harvey, 2016). Water pooling behind roughness features induces surface water to enter the hyporheic flow path upstream the structures (e.g. downward hyporheic flow) and to re-emerge downstream of the structures (e.g. upward hyporheic flow) or in sections of the stream where the slope is reduced (Lautz, Siegel & Bauer, 2006; Kasahara & Hill, 2006; Hester & Doyle, 2008). Both small and large hyporheic flow paths occur along streams, yet the greatest interaction with the stream results from relatively short hyporheic flow paths (Harvey & Wagner, 2000). Factors like sediment permeability (Hester & Doyle, 2008; Sawyer & Cardenas, 2009; Sawyer, Bayani Cardenas & Buttles, 2012), heterogeneity of streambed sediment hydraulic conductivity (Hester *et al.*, 2009; Menichino & Hester, 2014) and groundwater discharge (Storey *et al.*, 2003; Lautz *et al.*, 2006; Cardenas & Wilson, 2007b) control HEFs and associated hyporheic thermal patterns. Indeed, water fluxes into the hyporheic zone generally decrease during the wet season when higher groundwater levels generate greater opposition to fluxes into the streambed (Harvey & Wagner, 2000) forcing

exchange flow paths closer to the stream or even eliminating them (Wondzell, 2006), whereas vertical hyporheic exchange is greatest during low flow when topographic features have the largest effect on water-surface slope variability (Harvey, 2016). However, hyporheic exchange patterns and associated streambed thermal responses to fluctuating stream stage is more complex than the simplified model presented above, and more realistically, the hyporheic zone may present a range of temporal and spatial responses according to a variable gradation of stream-streambed connectivity and groundwater influence present in different regions of the streambed (Zimmer & Lautz, 2014).

Large wood is a key natural morphologic feature (Sawyer *et al.*, 2012; Sawyer & Cardenas, 2012) that increases vertical hydrological connectivity between river and groundwater ecosystems, primarily via hyporheic exchange flow (Lautz *et al.*, 2006; Kasahara & Hill, 2006; Mutz, Kalbus & Meinecke, 2007; Sawyer, Bayani Cardenas & Buttles, 2011). Also for this reason, among other benefits like geomorphic stability and heterogeneity (Faustini & Jones, 2003), enhanced aquatic habitat for biota (Gerhard & Reich, 2000) and biogeochemical cycling (Krause *et al.*, 2014), large wood is commonly installed in stream restoration projects (Hester & Gooseff, 2010; Roni *et al.*, 2015).

Main heat transfer mechanisms in streambeds are conduction and hyporheic advection (Cardenas & Wilson, 2007a; Hester *et al.*, 2009); and the amplitude of diurnal signal originating at the surface is attenuated and delayed with increasing depth in the subsurface (Briggs *et al.*, 2012). Because heat advection only occurs in the streambed where pore flowing water is present (Constantz, 2008), it is intuitive to understand that the relative importance of one heat transfer mechanism over the other is controlled by the sediment hydraulic conductivity (Menichino & Hester, 2014).

Although there is a growing body of streambed temperature research in lowland streams, no previous studies have provided a high-resolution characterization of spatio-temporal variability in seasonal streambed temperatures as they relate to changing hydroclimatological conditions and large wood. Briggs *et al.* (2012) collected continuously for one month during the summer high-resolution temperature data above two beaver dams to investigate hyporheic exchange dynamics induced by the dams at different morphological features. They observed a variation in magnitude of heat transport into the subsurface and vertical flux patterns by location (e.g. with streambed morphology and distance from the dams), and through time (e.g. with decreasing discharge). This suggests that seasonal variability in hydrological conditions may exert a considerable influence on streambed thermal dynamics of a lowland stream; perhaps because the stream mosaic of patches of vertical hydrological exchange is continuously modified and reconfigured by natural mechanisms of geomorphological change (e.g. sediments transport) in response to the pulsing of discharge (Boulton, 2007).

To address the above research gaps, this paper compares high-resolution streambed temperatures distribution in a lowland forested stream reach in the UK across multiple locations (e.g. in space) over different monitoring periods (e.g. in time). The study aims to improve understanding of the driving conditions and processes that affect the magnitude of seasonal spatio-temporal changes in streambed temperatures of a natural stream. The specific hypotheses tested are:

- i. seasonal variability in streambed temperatures is driven by changes in stream stage and localized hydroclimatological conditions;
- ii. temperature patterns observed in the streambed during the summer reverse during the winter;

- iii. locations around the woody structures present increased streambed temperature variability due to wood-enhanced hyporheic exchange flow compared to locations far away from large wood.

5.2 METHODS

5.2.1 STUDY AREA

This study was conducted in the Hammer Stream, a sandy tributary of the River Rother in West Sussex, UK (Figure 15). The Hammer catchment has a total area of 24.6 km² and its geology comprises Greensands and Mudstones, with agriculture and mixed broadleaved woodland being the dominant land uses. The stream channel has a meandering morphology and in some sections natural large wood accumulation (e.g. logs, branches and wood fragments > 10 cm in diameter and 1 m in length) and log jams can be found. Occasionally, after prolonged and heavy rainfall events typically during the autumn and winter season, the Hammer Stream shows flashy responses, so that a rapid increase in runoff can be observed. Consequently, the less stationary component of wood is mobilized and transported downstream.

The ~40-m long study reach was located in a deciduous forested valley, characterized by sand-dominated streambed sediments. Along this reach, the presence of three prominent and stable, several year-old woody structures each spanning > 50% of the channel width (LWD, Figure 15) created storage sites for sediments accumulation behind wood, increasing the heterogeneity of bed elevation and water depth. Ground penetrating radar (GPR) surveying complimented by data from sediments cores (not presented here) carried out at the study reach revealed the presence of extensive clay lenses and peat layers at 1-2 m depth that effectively

isolate the upper streambed from the underlying groundwater. Therefore, surface water downwelling together with bank flow contribution is the dominant hyporheic flow.

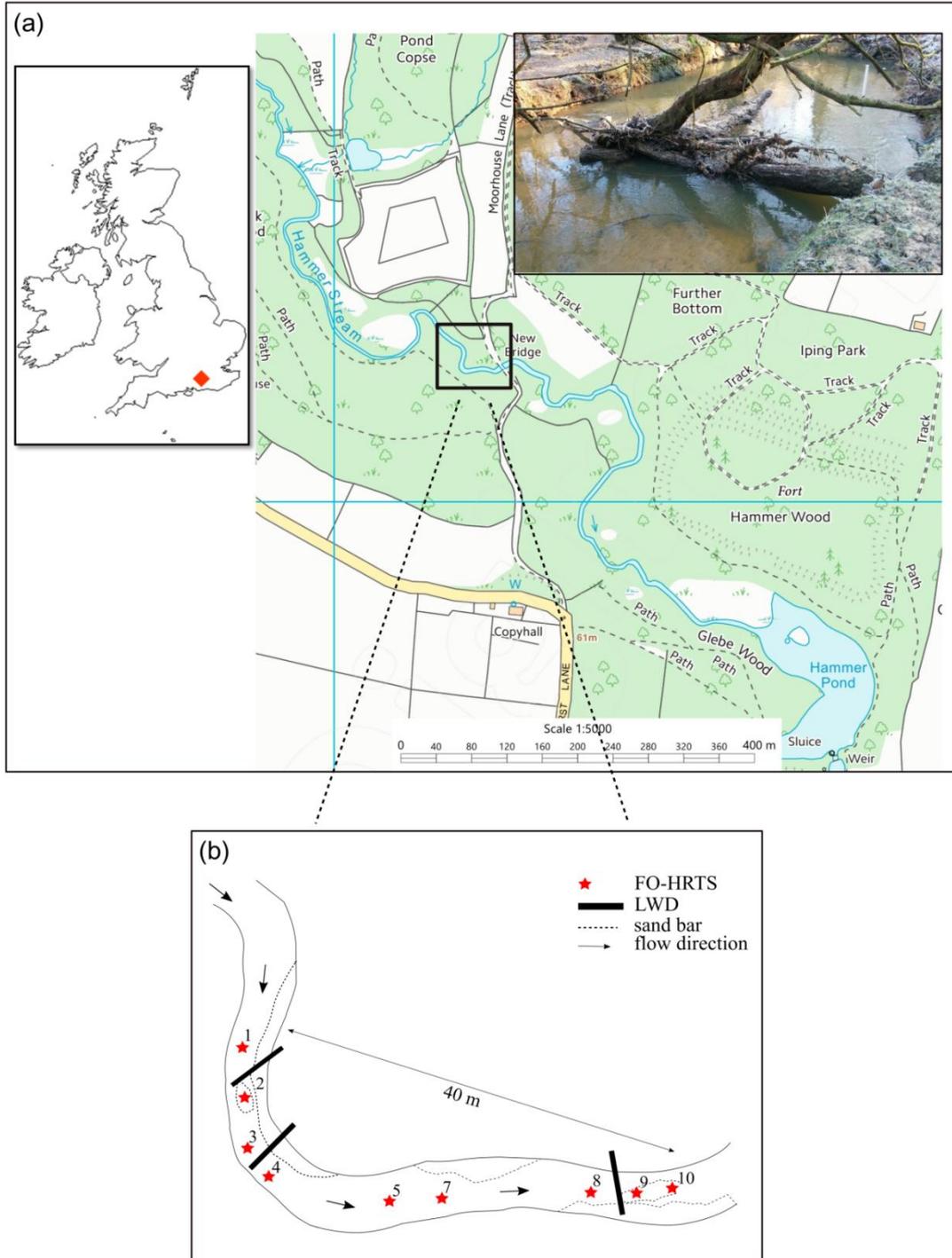


Figure 15. Location of the study site in the UK and within the forested valley with a photograph of the most downstream woody structure (a); the 3 woody structures at the study reach with the high-resolution temperature sensor (HRTS) locations (b).

5.2.2 EXPERIMENTAL SET UP AND DATA COLLECTION

5.2.2.1 HYDROCLIMATOLGICAL MONITORING

Stream water level, together with surface water and air temperature were monitored continuously from June 2015 to January 2016 with readings recorded every 15 min using a pressure transducer (Levelogger 3001, Solinst, Ontario, Canada), and compensated for changes in atmospheric pressure changes by a barometer (Barologger Edge, Solinst, Ontario, Canada; temperature sensor accuracy was ± 0.05 °C, level sensor accuracy $\pm 0.05\%$ FS). These data were provided by the NERC project NE/L004437/1.

Daily precipitation totals were obtained from a weather station (Iping Mill station, National Centre for Atmospheric Science, Natural Environment Research Council, Met Office Integrated Data Archive System) approximately 1.5 miles from the site.

5.2.2.2 HIGH-RESOLUTION STREAMBED TEMPERATURES MONITORING

A total of nine HRTS (ten HRTS were in reality installed, but it was found out later on that one had a cable damage, so it was by-passed) were inserted vertically into the streambed sediments (see Chapter 3 for a detailed description of HRTS) at locations indicated in Figure 15 by gently pushing them into the soft sandy sediments in November 2014. Installation locations were chosen to best represent and cover the heterogeneity of channel morphological features (Table 13).

Table 13. Morphology and short description of the location of HRTS installation.

HRTS	Morphology	Details
1	Glide	
2	LWD 1	Downstream, middle of a sandbar
3	LWD 2	Upstream
4	LWD 2	Downstream
5	Glide	
7	Glide	
8	End of glide	Edge of a lateral sandbar
9	LWD 3	Downstream, head of a sandbar
10	Bar	Tail of a sandbar

The HRTS were connected in two distinct series using a Fujikura 19S Fusion splicer: the first loop comprised HRTS from 1 to 5 ($n = 5$), and the second loop from 7 to 10 ($n = 4$) (Figure 15). The choice of having two loops instead of one as done in Chapter 3 and 4 was justified by harsher environmental conditions compared to those for laboratory experiments and by the necessity of keeping the experimental set up stable and unaltered over 1-year time. In fact, in this way, if one loop was damaged and thus not monitoring temperatures, the other one would keep on measuring, thus the risk of losing data was reduced and maintenance easier with fewer HRTS connected in one single loop. Distinct temperature signals were applied to the cables at known reference points (e.g. before the cable of each HRTS entered the streambed and straight after it exited it) to locate the position of each HRTS along the entire cables length. Because not all HRTS were completely into the streambed, the surface water-streambed interface (hereafter WSI) was identified for each HRTS during each sampling occasion (except in January 2016 when high water level prevented safe access to the stream at some locations), and local water level monitored as well. Progressive sediments deposition or scouring occurred at different location in time, therefore it was essential to periodically monitor for change of interface position.

To make sure the metres of cables left at the top of each HRTS (~20 m) to allowing in series connections would not be damaged by the transport of new wood inputs from upstream reaches during high flow events or floods, these were protected by placing them in rubber hose pipes, pegged to the streambed or buried where possible (Figure 16). For the same reason, fusion splices between two consecutive HRTS were protected by housing them in waterproof-designed splice boxes, fixed to the streambed or stable wood using robust string.

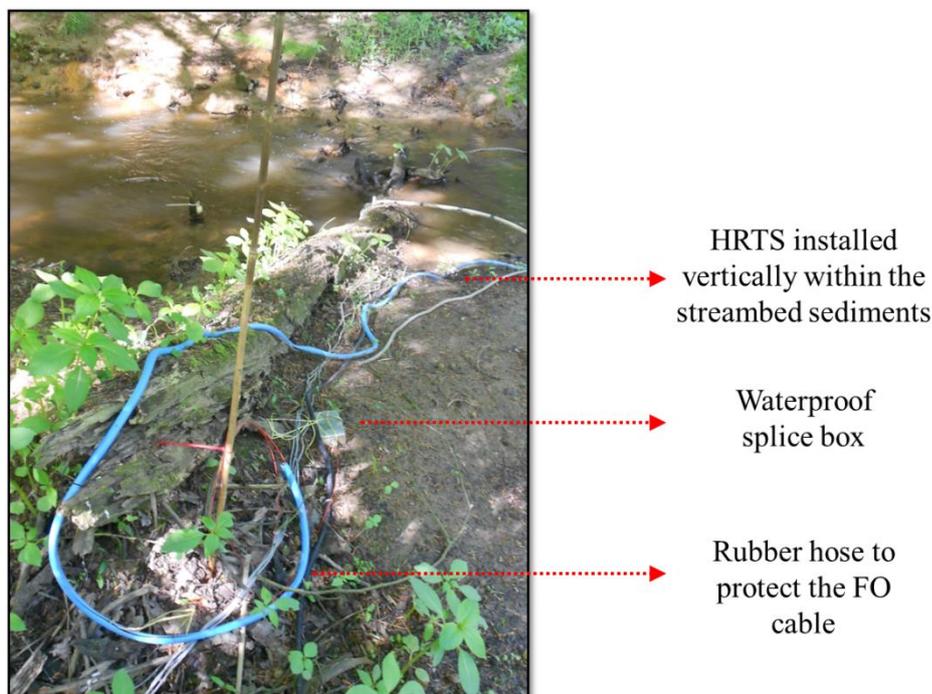


Figure 16. Rubber hose pipes protected the FO cables and waterproof boxes housed fusion splices.

Given the complexity of the experimental set up together with the extremely time-consuming and delicate process of housing the cables in hose pipes and next reliable, accurate splicing operations under variable hydrological conditions, the two loops of HRTS were ready to securely operate from June 2015.

Streambed temperature measurements were carried out at the study site on four occasions (Table 14).

Table 14. Overview of the sampling periods and corresponding dates.

Year	Monitoring season	Dates of monitoring period
2015	Early summer	13/06 (09:52) – 19/06 (11:23)
	Summer	01/07 (13:42) – 03/07 (12:00)
	Autumn	02/11 (11:41) – 05/11 (22:52)
2016	Winter	18/01 (22:05) – 21/01 (16:12)

The DTS unit (XT-DTS™, Silixa Ltd, UK) was run in single-ended mode with alternating measuring directions (Krause & Blume, 2013) for each of the single loop during dates indicated in Table 14. The DTS acquisition interval was 30 s per channel (e.g. 60 s in total were required to sense one loop - two channels - in both directions, thus time interval between measurements from the same channel was 2 min) and the sampling resolution was 0.25 m along the fibre (e.g. this translated into 0.004 m sampling vertical resolution using HRTS). Both differential loss (per each loop and direction) and temperature offset between measured and true temperatures were dynamically calibrated at each 30-s measurement. Differential loss was calculated by matching temperatures in two reference sections (two for each loop) that were placed in an ambient temperature water bath kept mixed continuously by a bilge pump over the time of data sampling, while temperature offset was accounted by placing one of the two temperature probes supplied with the DTS unit in the same water temperature bath of the reference sections. Two 12-V, 50-Ah batteries connected in series were necessary to power the DTS system, and these were swapped with a couple of fully charged batteries every 12 hours maximum. Another 12-V battery was used to power the bilge pump. When in operation, the DTS instrument was protected inside a camping tent.

5.2.3 DATA ANALYSIS

5.2.3.1 HYDROCLIMATOLOGICAL DATA

Air and water temperatures (°C) at the site were evaluated including temperature metrics like mean±SD, maximum, minimum for each monitoring period (Table 14); yet, to give a broader overview mean±SD, maximum, minimum and variance for the whole month in which each sampling was carried out (e.g. June, July, November 2015 and January 2016) were also considered. In addition, the magnitude of change in both air and surface water diurnal temperatures range (DTR) - obtained by subtracting daily minimum temperature from daily maximum temperature - was examined throughout each monitoring month as well. Differences in variation in diurnal surface water temperature cycles among monitoring months were investigated using one-way Anova followed by a Tukey's *post-hoc* comparisons test.

Similarly, water level (m) at the site was described including variables like mean±SD, maximum and minimum for each monitoring period, together with mean±SD, maximum, minimum and variance for each monitoring month.

Precipitation inputs (mm) were characterized by employing daily precipitation totals throughout each monitoring period.

5.2.3.2 HIGH-RESOLUTION STREAMBED TEMPERATURE PROFILES

For each monitoring period, streambed temperature for each 2 min timestep averaged over 20-min was plotted by depth through time along each HRTS to explore streambed temperature distributions at each location. Some gaps in the data were present due to equipment malfunctions that were between 13h:33min during monitoring period in June and 2h:10min

during monitoring period in November (the last gap involved only HTRSs from 1 to 5). These data gaps were treated as missing values.

5.2.3.3 SURFACE WATER TEMPERATURE INFLUENCE ON STREAMBED TEMPERATURES

Pearson's product moment correlation coefficients (r) were estimated to investigate potential association between surface water and streambed temperatures as a measure of surface water influence. The strength and significance of association were explored for every depth along each HRTS up to 0.65 m during each monitoring period (e.g. 0.65 m is the absolute minimum depth reached by HRTS 9 during monitoring period in June); streambed temperature were averaged every 20 min and surface water temperature monitored every 15 min was interpolated at 20-min intervals. All correlations were significant when $P < 0.01$.

5.2.3.4 INFLUENCE OF LARGE WOOD ON SEASONAL SPATIO-TEMPORAL MEANS OF STREAMBED TEMPERATURES

Streambed temperatures up to 0.65 m for each HRTS were averaged over each entire monitoring period (e.g. over time) and were used to produce mean streambed temperature profiles, but distinguishing between HRTS around or in close proximity to large wood (HRTS 2, 3, 4, 9) and those farthest away (HRTS 1, 5, 7, 8, 10).

A mean value over depth (e.g. over space, from WSI up to 0.65 m depth) of streambed temperature averaged over time for each HRTS was also calculated (e.g. spatio-temporal mean). In this way, a total of 36 values of spatio-temporal means of streambed temperatures (9 HRTS by 4 monitoring periods) were obtained. To test for differences in seasonal spatio-temporal means of streambed temperatures between HRTS around the woody structures and those away from the LWD a linear mixed effect models with Gaussian error distribution

(LME) was used followed by a Tukey's *post-hoc* comparisons test. The spatio-temporal mean of streambed temperature during each monitoring period for each HRTS was treated as the response variable, the proximity/non-proximity of large wood and the monitoring period as fixed effects; HRTS was considered as a random effect. Statistical tests were performed using the *nlme* (Pinheiro *et al.*, 2016) and *lsmeans* packages (Lenth, 2016) in R 3.3.1 (R Core Team, 2016).

5.3 RESULTS

5.3.1 HYDROCLIMATOLOGICAL DATA

Air temperature (air T) at the site displayed a clear seasonal trend (Figure 17) and varied on a sub-daily basis with different incoming radiation receipts. Within all monitoring periods, air temperature peaked in July when the maximum value of 28.52 °C was registered (Table 15), while minimum temperature was observed in January (-6.13 °C). Mean (\pm SD) monthly air temperature was 14.37 \pm 3.82 °C, 15.79 \pm 3.68 °C, 10.20 \pm 3.80 °C and 5.21 \pm 3.94 °C for June, July, November 2015 and January 2016 (Table 16), respectively, while mean air temperature restricted to each monitoring period is given in Table 15.

Table 15. Mean value (\pm SD) for water level (m), water and air temperature (°C) and total precipitation (mm) during each monitoring period. Minimum and maximum values are given in brackets.

Date	Water level (m)	Water T (°C)	Air T (°C)	Tot. precipitation (mm)
13 - 19/06/15	0.69 \pm 0.07 (0.62 - 1.01)	13.7 \pm 0.8 (12.2 - 16.1)	14.85 \pm 3.19 (8.01 - 21.51)	24.2
01 - 03/07/15	0.61 \pm 0.01 (0.59 - 0.63)	16.1 \pm 0.8 (14.9 - 17.7)	19.05 \pm 4.48 (9.13 - 28.52)	0.4
02 - 05/11/15	0.75 \pm 0.09 (0.70 - 1.32)	11.2 \pm 0.4 (10.9 - 12.4)	11.72 \pm 1.59 (8.651 - 14.38)	6.2
18 - 21/01/16	0.91 \pm 0.08 (0.81 - 1.05)	4.1 \pm 0.9 (3.0 - 5.4)	-0.21 \pm 3.57 (-6.13 - 6.83)	na

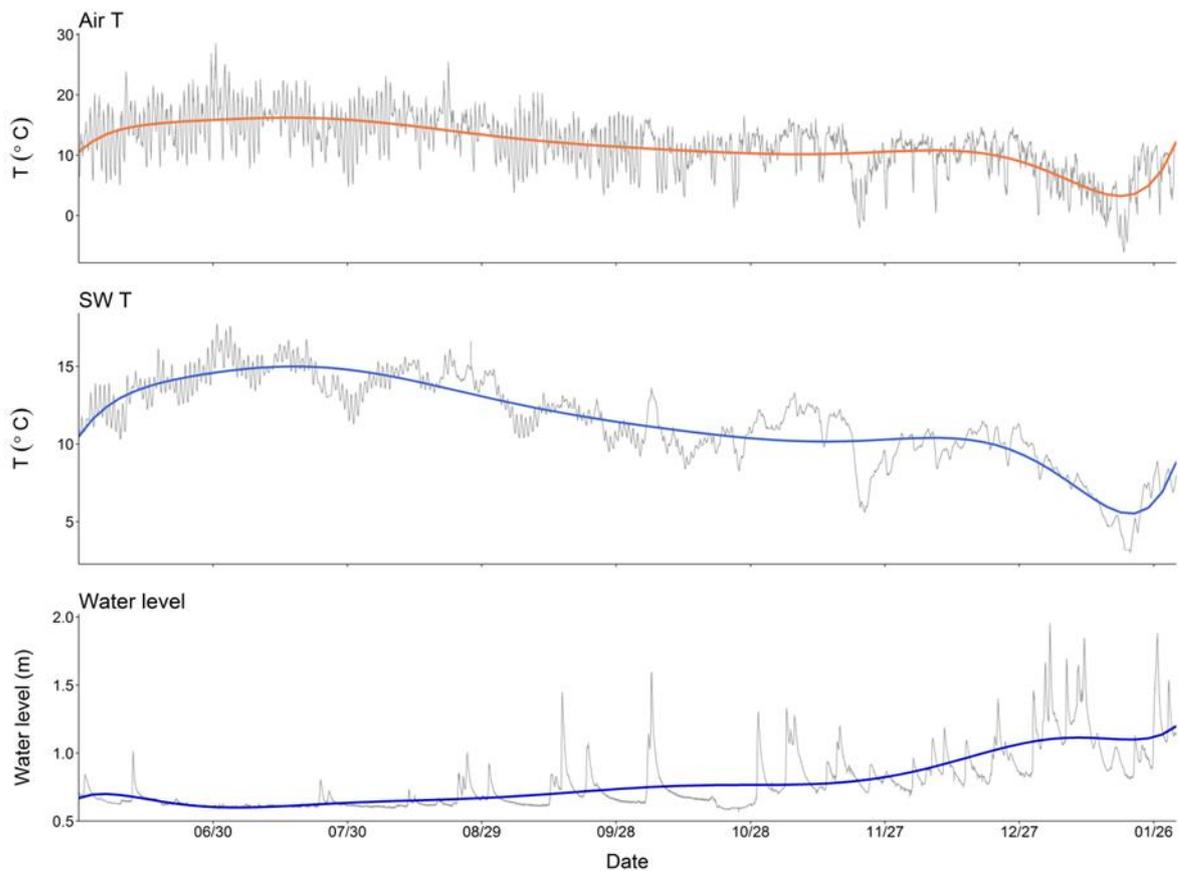


Figure 17. Air (Air T, °C) and surface water (SW T, °C) temperature with water level (m) from June 2015 to January 2016.

Variations of mean monthly air temperatures were similar among monitoring months, being 14.62, 13.56, 14.47 and 15.49 for June, July, November 2015 and January 2016, respectively (Table 16). The biggest magnitude of variation in air DTR was generated in June (30/06/15, 17.79 °C) that corresponded also to the period during which monthly average air DTR was the widest (9.77 ± 3.38 °C), whereas the smallest change was obtained in November (05/11/15, 1.24 °C).

Table 16. Mean monthly temperature (\pm SD), variance and range of DTR variation ($^{\circ}$ C) for air and surface water during each monitoring month.

	Monitoring month	Mean T\pmSD ($^{\circ}$C)	Variance T ($^{\circ}$C)	Range of DTR variation ($^{\circ}$C)
Air T	June 2015	14.37 \pm 3.82 (5.04 – 26.85)	14.62	4.93 – 17.79
	July 2015	15.79 \pm 3.68 (4.81 – 28.52)	13.56	2.02 – 15.91
	November 2015	10.20 \pm 3.80 (-2.05 – 16.08)	14.47	1.24 – 8.60
	January 2016	5.21 \pm 3.94 (-6.13 – 12.13)	15.49	1.97 – 11.17
SW T	June 2015	13.2 \pm 1.3 (10.3 – 16.7)	1.75	0.7 – 3.6
	July 2015	14.9 \pm 1.2 (11.5 – 17.7)	1.36	0.4 – 2.8
	November 2015	10.4 \pm 2.0 (5.6 – 13.3)	3.93	0.2 – 2.7
	January 2016	6.7 \pm 1.6 (3.0 – 9.3)	2.52	0.3 – 1.6

Mean (\pm SD) monthly surface water temperature (SW T) was 13.2 \pm 1.3, 14.9 \pm 1.2, 10.4 \pm 2.0 and 6.7 \pm 1.6 $^{\circ}$ C for June, July, November 2015 and January 2016 respectively, with the maximum value of 17.7 $^{\circ}$ C registered in July and the minimum value of 3.0 $^{\circ}$ C in January (Table 16). Mean values during each monitoring period are given in Table 15. Variances of mean monthly surface water temperatures were greater in November and January (3.93 and 2.52, respectively) than during summer season (1.75 and 1.36 for June and July, respectively), indicating that mean monthly surface water temperatures varied more during autumn and winter time, less in summer time.

Diurnal cycles of surface water temperature were evident at the site and these were buffered and lagged relative to air DTRs (Figure 17, Table 16). Investigations of surface water DTRs established that they varied in magnitude with season ($P < 0.0001$), with June showing the widest monthly average surface water DTR (1.9 \pm 0.7 $^{\circ}$ C) among all monitoring months (Figure 18).

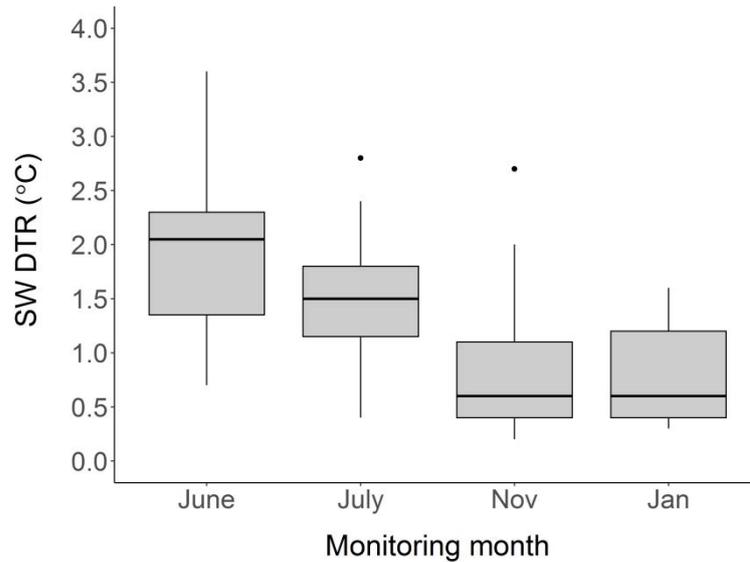


Figure 18. Median of DTR for surface water (°C) during each monitoring month.

A Tukey's *post-hoc* comparisons test revealed statistically significant differences between surface water DTRs obtained during summer and colder monitoring months ($P < 0.0001$; June vs. November, June vs. January, July vs. November and July vs. January), differences in surface water DTRs between summer monitoring months were also statistically significant ($P = 0.0023$; June vs. July), while differences between DTRs of November vs. January were not significant.

Mean (\pm SD) and ranges for water level during each monitoring period are shown in Table 15. Mean monthly water level was 0.66 ± 0.06 , 0.62 ± 0.03 , 0.85 ± 0.13 and 1.15 ± 0.24 m during June, July, November 2015 and January 2016, respectively. Diurnal fluctuations were particularly visible during November and January (Figure 17) - up to 0.72 m daily water level variation in January - when water level displayed major responses to frequent and intense rainfall events, resulting in increased flow at the site.

5.3.2 HIGH-RESOLUTION SEASONAL STREAMBED TEMPERATURE VARIABILITY

Scouring and deposition of fine sediments due to seasonal hydrological dynamics changed WSI position in time at locations where HRTS were placed. For this reason, the maximum depth in the streambed sediments reached by each HRTS differed among monitoring periods, with 0.65 m being the absolute minimum depth reached by HRTS 9 in June. During data post processing, sections of HRTS above the WSI (e.g. in the air, stream water or buried in dry sediments) were removed from the analysis.

Manual water level measurements (cm) taken in correspondence of each HRTS location are presented in Table 17.

Table 17. Water level (cm) as measured manually at each location during each monitoring period (* indicates the sediment was raised above the water table behind the LWD in which the HRTS was buried; Na indicates water level is not available).

	HRTS	Monitoring period			
		13 – 19/06/15	01 – 03/07/15	02 – 05/11/15	18 – 21/01/16
Water level (cm)	1	32.0	28.0	47.0	Na
	2	1.3*	0.0	13.0	4.5*
	3	9.2	3.0	20.5	27.0
	4	6.2	3.0	16.0	Na
	5	20.0	16.5	37.5	Na
	7	36.0	32.0	51.5	Na
	8	12.5	9.5	22.5	29.5
	9	26.0*	2.0*	3.0	16.0*
	10	3.5	0.5	24.5	Na

20-min average streambed temperatures obtained from every HRTS using values for each 2 min timestep at 0.004 m spatial resolution differed from one monitoring period to another, with streambed thermal regimes exhibiting marked spatio-temporal variability.

During the summer, at or near base flow, when the stream thermal capacity was reduced, for all HRTS higher streambed temperatures were observed in the shallow sediments and lower streambed temperatures were measured in the deeper sediments, reflecting the existence of notable negative temperature gradients in the sediments with depth. Distinct diel cycles of streambed temperatures were visible in the shallow sediments up to a depth that varied with the location of each HRTS, while deeper sediments displayed constantly cooler temperatures. Furthermore, the intensity of shallow streambed sediments warming during day-time and cooling at night resulted from air and surface water DTRs, denoting a strong influence of surface hydroclimatological conditions on the thermal regime of shallow streambed sediments.

In June throughout 6-day measurements (13-19/06/15), streambed temperatures from WSI to maximum 1 m depth in the sediments (HRTS 3, 5 and 7) ranged from 18.2 to 10.5 °C (Figure 19). Upper thermal limit of streambed sediments temperature range (18.2 °C) was 2.1 °C greater than upper limit of surface water temperature range (16.1 °C, Table 15) during the same period, denoting different localized water level conditions at varying location, thus the occurrence of a small-scale heterogeneity of stream thermal capacity. The intensity of diurnal warming reaching the streambed sediments increased from the first to the last day of measurements due to a general increase in maximum air temperatures during the same period combined with a continuous decrease in mean water level that passed from 0.84±0.09 m on 13/06/15 to 0.63±0.01 m on 19/06/15 (Figure 19). This greater rate of heat gradually transferred to the streambed sediments via combined conduction and advection implied a greater depth of penetration of the surface temperature signal with time, and especially for HRTS at slow-flow locations where water level was also exceptionally low (e.g. HRTS 10). The thermal damping depth of ~14.5 cm with a thermal diffusivity for sandy soil of 0.75×10^{-6}

m^2/s (Krause *et al.*, 2011a) was calculated in the case of pure conduction; this means that, according to the theoretical calculation of the damping depth of a penetrating periodic thermal signal, the amplitude of the streambed temperatures should only be 37% of the river's temperature fluctuations at 14.5 cm below the WSI (Hillel, 1998). However, a decay of 37% of the mean stream temperature amplitude was not observed at least until 0.33 m below the WSI, indicating that advection was an important transport mechanism. Shallow streambed sediments distinctly showed 6 diel temperature cycles, and temperatures markedly dropped at night time in two occasions (16 and 17/06/15) when minimum air temperature values decreased consistently. In fact, on 16 and 17/06/15 a negative temperature difference of 4.01 and 2.76 °C, respectively relative to the highest value for minimum air temperature recorded on 13/06/15 was registered. For HRTS 3 that was located immediately upstream the second large wood, surface water temperature signal penetrated deeper into the streambed than HRTS 4 located immediately downstream the woody structure. 0.5 m below the WSI mean streambed temperature was 12.9 ± 0.2 °C for HRTS 3, but the same mean streambed temperature was found at 0.32 m depth for HRTS 4, suggesting that wood, being an obstruction that can cause variations of the local water level, induced stream-hyporheic water exchange. This intensified stream-hyporheic coupling due to the presence of wood resulted in an expanded hyporheic zone for HRTS immediately downstream large wood (e.g. HRTS 2 and 4).

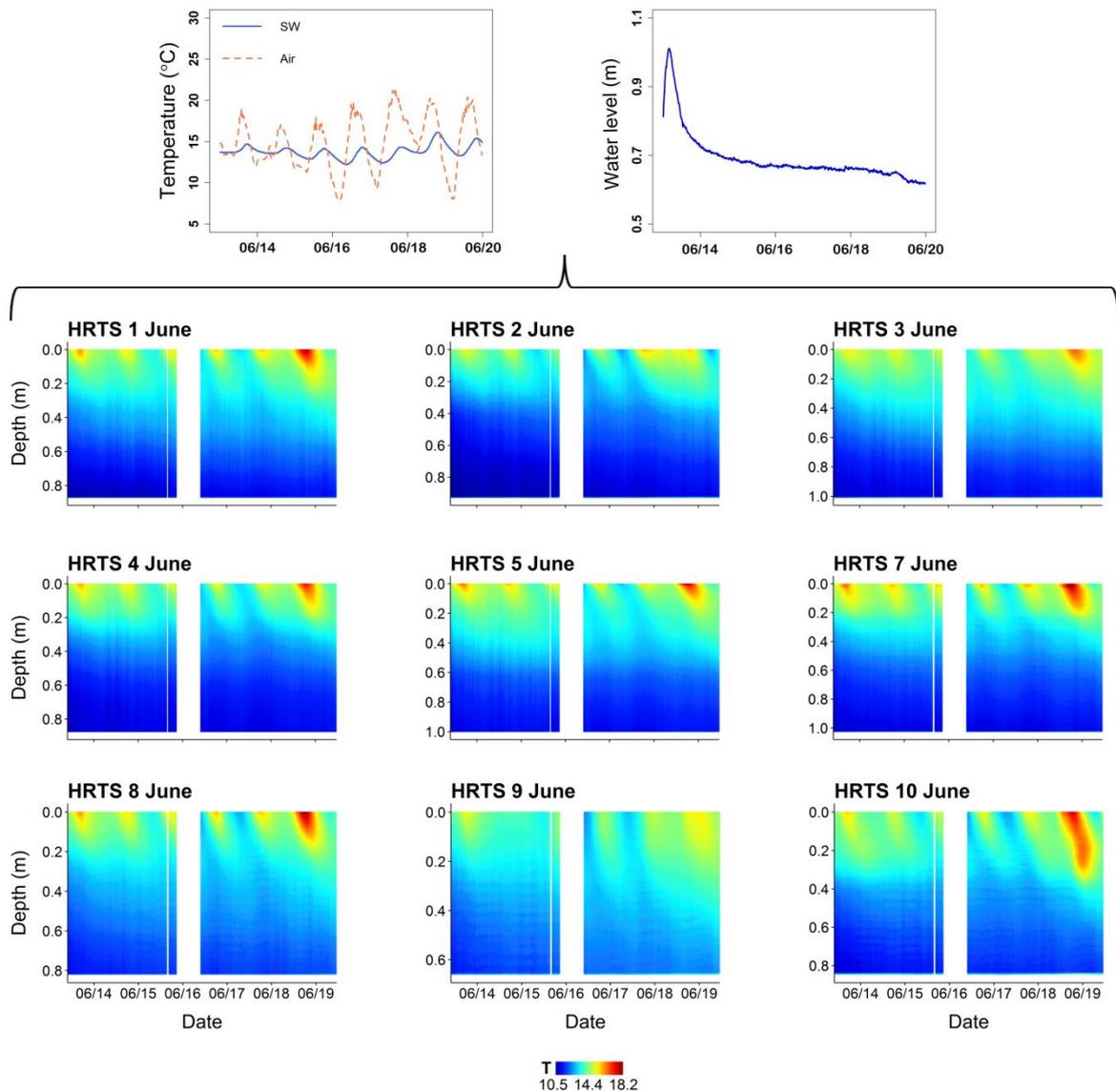


Figure 19. Time series of surface water temperature, air temperature and water level with 20-min average streambed temperature at 0.004 m spatial resolution through time at all locations of the study reach for the monitoring period 13-19/06/15.

During monitoring period in July (01-03/07/15), water level at the site decreased up to a minimum value (0.59 m) very close to the absolute minimum water level (0.57 m) recorded at the end of October, and the DTS unit was in function when the absolute maximum value for air temperature at the site (28.52 °C) was registered (01/07/15 ~14:30). Although sediments remained saturated, water level in correspondence of each HRTS dropped dramatically and in particular at higher topographic locations produced by the depositions of fine sediments

behind wood (e.g. for HRTS 2, 9 and 10). As a consequence, both lower and upper limit of streambed temperatures range increased, by 1.1 and 2.0 °C from June, respectively, becoming 11.9 and 20.2 °C (Figure 20), while upper limit of streambed temperature range was 2.5 °C greater than the one of surface water temperature range during the same period. Throughout the 2-day monitoring period, the intensity of warming reaching the shallow sediments increased relative to previous monitoring period in June, and water level between upstream and downstream woody structures locations became more similar. Therefore, the pattern observed in June of stream temperature signal propagating to greater depths for HRTS 3 located upstream the large wood than HRTS 4 located downstream was no longer present, most likely because no gradient in hydraulic head was present between these two locations.

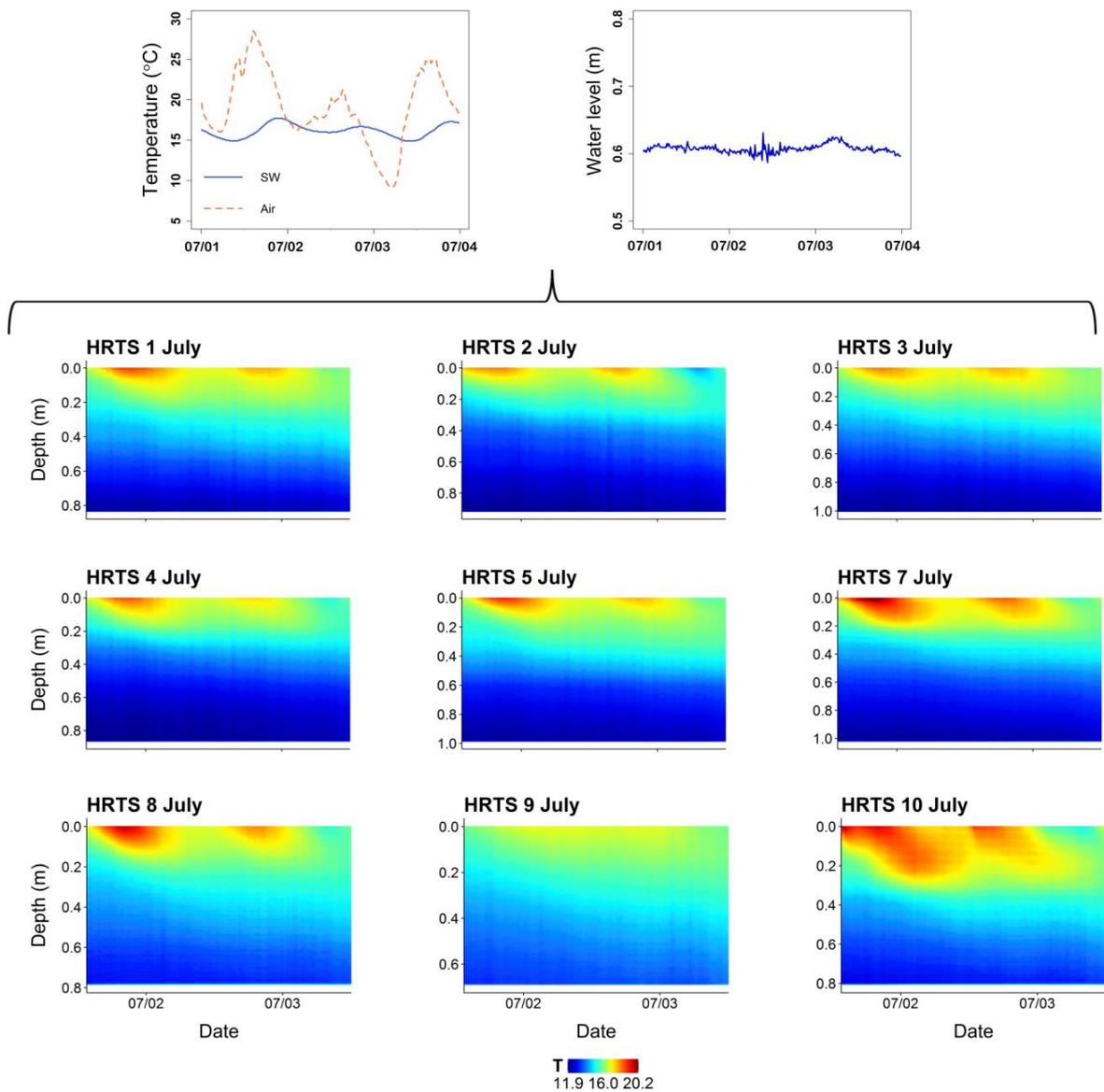


Figure 20. Time series of surface water temperature, air temperature and water level with 20-min average streambed temperature at 0.004 m spatial resolution through time at all locations of the study reach for the monitoring period 01-03/07/15.

During the autumn, little (negative) or no thermal gradients were observed, resetting streambed thermal regimes. On average, streambed temperatures were very similar to the mean stream water temperature for the same period. A storm event occurred on 05/11/15 in the night time, and it impacted streambed temperatures differently at varying location.

During monitoring period in November (02-05/11/15) streambed temperatures from the WSI up to 1 m depth (HRTS 3, 4, 5 and 7) ranged from 13.3 to 10.8 °C (Figure 21), the smallest temperature range among all monitoring periods.

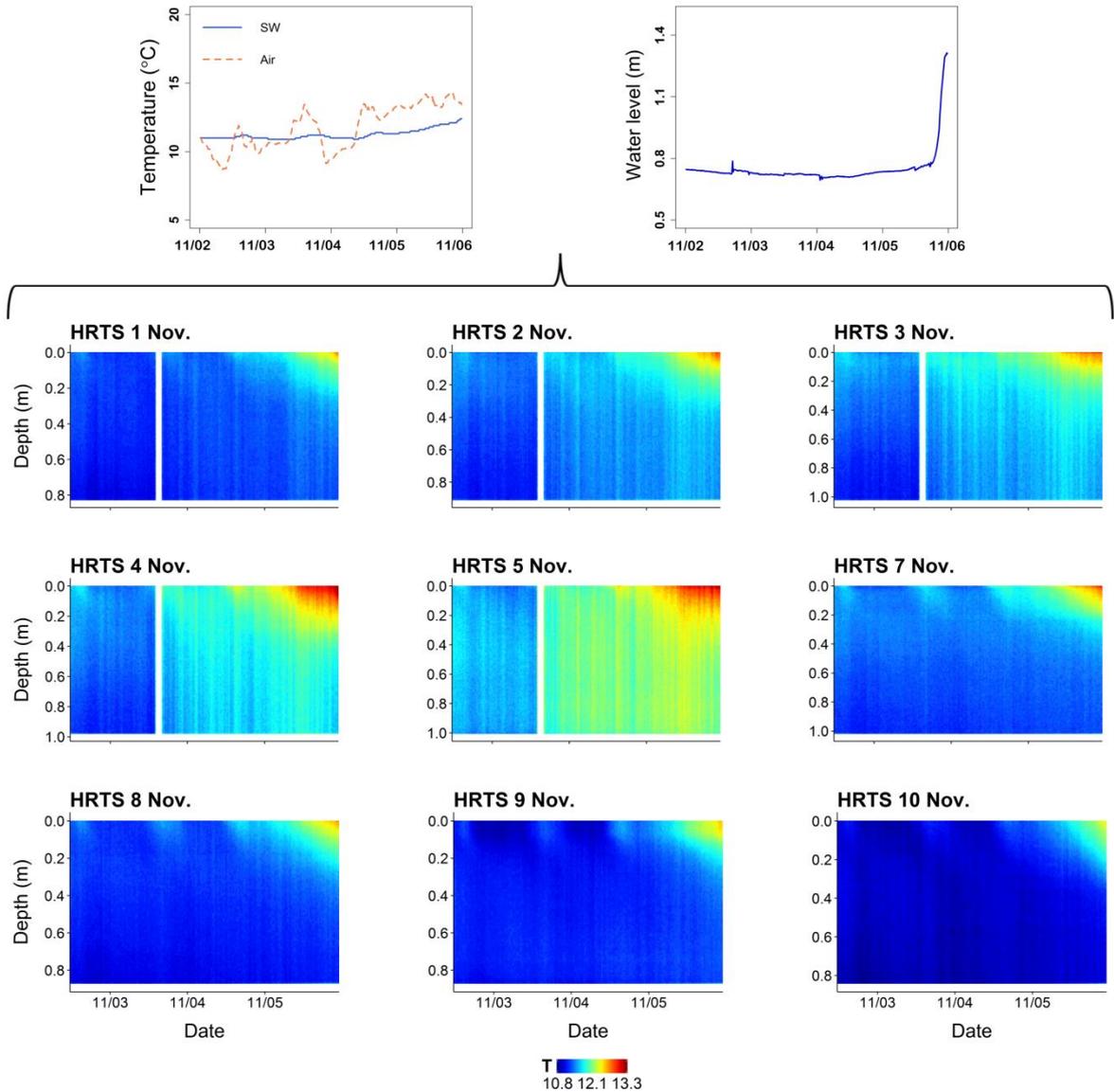


Figure 21. Time series of surface water temperature, air temperature and water level with 20-min average streambed temperature at 0.004 m spatial resolution through time at all locations of the study reach for the monitoring period 02-05/11/15.

Values of both air and surface water DTRs prior the storm event were all similar, during the peak event (night hours on 05/11/15) air DTR decreased (e.g. a smaller difference between

maximum and minimum air temperature values was observed), whereas surface water DTR increased (e.g. both values for maximum and minimum surface water temperature increased, but the magnitude of change for maximum temperature was bigger, meaning on the whole warmer surface water). In summary, on 05/11/15 the concomitance of mean daily warmer air with significant amount of warmer water inputs contributed to induce a streambed thermal response which temperature footprint varied in depth with location. Stream water seemed to infiltrate along a preferential flow path at HRTS 2, into the meander bend, and to converge towards HRTS 5, at the end of point bar. Likely, the presence of the top two woody structures, the downstream decrease in bed topography from HRTS 2 to HRTS 5 (see Shelley *et al.*, 2017, Figure 7) and the stream meander bend together were conducive to the resulting thermal pattern observed at these locations.

During the winter, under high-flow stream conditions, remarkable positive temperature gradients in the streambed were detected, with lower temperatures observed in the shallow sediments and higher temperatures in the deeper sediments, so, totally reversing the streambed temperature patterns observed during the summer. Unfavourable prevailing surface hydroclimatological conditions affected shallow streambed sediments only, while deeper streambed sediments were effectively buffered and presented constantly warmer streambed conditions.

During monitoring period in January (18 - 21/01/16), streambed temperatures from WSI to 1-m depth (HRTS 1, 3, 4, 5, 7, 8 and 10) ranged from 1.2 to 9.4 °C (Figure 22). Upper limit of streambed temperature range was 4.0 °C greater than the one of surface water temperature range, denoting warmer temperature conditions in the deeper sediments than surface water. A substantial continuous decrease in minimum air temperature from 18/01 to 20/01/16 (from -1.71 to -6.13 °C, respectively) resulted in a gradual decrease in mean daily surface water

temperatures during the same period (from 5.3 to 3.2 °C, respectively); this affected streambed temperatures as well, as temperature of the shallow sediments got gradually cooler throughout the monitoring period. However, for HRTS located around large wood (HRTS 2, 3, 4 and 9) temperatures of the shallow sediments decreased through time but to a lesser degree compared to HRTS located at a greater distance from wood (HRTS 1, 5, 7, 8 and 10). This suggested that the hyporheic exchange was enhanced around the woody structures when river discharge was high.

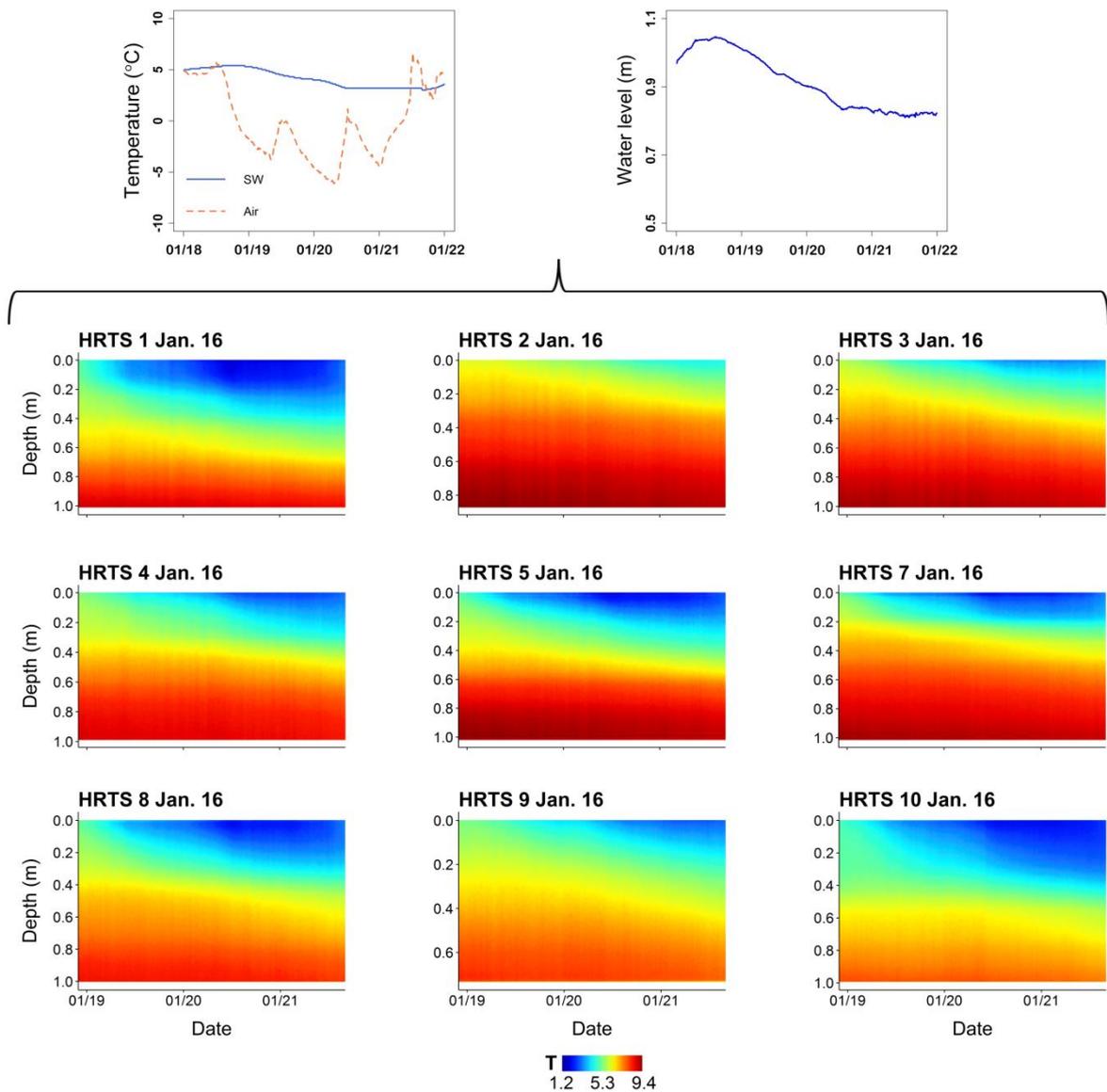


Figure 22. Time series of surface water temperature, air temperature and water level with 20-min average streambed temperature at 0.004 m spatial resolution through time at all locations of the study reach for the monitoring period 18-21/01/16.

5.3.3 SURFACE WATER TEMPERATURE INFLUENCE ON STREAMBED TEMPERATURES

Correlations between streambed temperature at every depth and surface water temperature with $P < 0.01$ were plotted by depth for each HRTS, and consistent patterns among locations within the same period were evident.

During the summer, correlation between surface water and streambed temperatures was high in the shallow sediments at all locations, indicating strong surface water influence. Yet, the strength of relationships strongly decreased with depth, suggesting reduced surface water temperature controls with increasing depth. In June, the strongest correlation was for HRTS 3 at 0.004 m depth ($r = 0.998$), followed by HRTS 8 at 0.08 m ($r = 0.995$), while the weakest was for HRTS 5 at 0.56 m depth ($r = -0.158$). At a mean depth of 0.28 m in the streambed r values were ≤ 0.300 ; for HRTS 10, r value ≤ 0.300 was found at a depth of 0.40 m, while the same r value was found at the shallowest depth of 0.23 m for HRTS 5 (Figure 23).

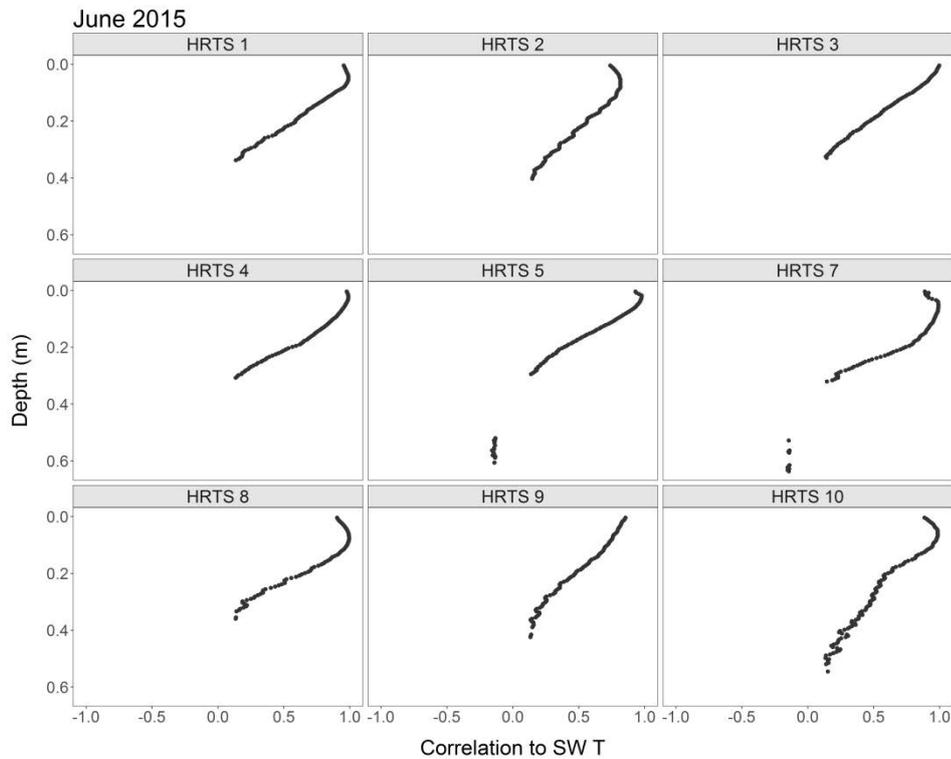


Figure 23. Significant correlation coefficients ($P < 0.01$) for each HRTS during 13-19/06/15.

In July (Figure 24), within the upper 0.1 m of the bed the strongest correlation was for HRTS 7 at a depth of 0.06 m ($r = 0.997$), followed by HRTS 5 at 0.02 m depth ($r = 0.997$). Compared to previous monitoring period, the strength of association between surface water and streambed temperatures decreased more intensely with depth, and in the deeper sediments

all HRTS had strong negative correlation to surface water temperature (r values more negative than -0.500), indicating different mechanisms controlling streambed temperatures between shallow and deeper sediments as water level drastically decreased (groundwater contributions were excluded due to the presence of extensive clay lenses and peat layers at 1-2 m depth, see 5.2.1 Study area section). With flow reduction, the transport of detritus and fine sediments normally stops, giving rise to accumulation and trapping of fine sediments into pools (Lake, 2003) which can increase streambed permeability heterogeneity. This in turn increases the complexity of hyporheic exchange paths (Sawyer & Cardenas, 2009).

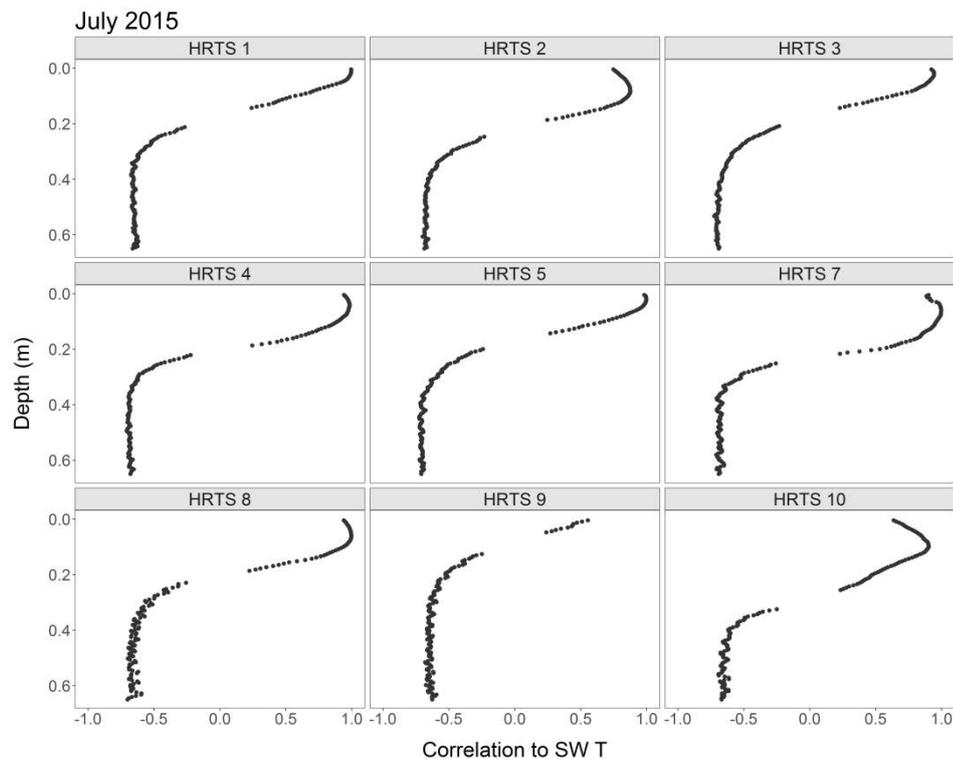


Figure 24. Significant correlation coefficients ($P < 0.01$) for each HRTS during 01-03/07/15.

During monitoring period in November and in January, streambed sediments for all HRTS showed strong and positive relationships with surface water up to 0.65 m depth in the streambed, suggesting greater surface water influence in the autumn and winter as river stage increased.

In November (Figure 25), the strongest association was for HRTS 10 at 0.04 m depth ($r = 0.990$), followed by HRTS 8 at 0.06 m depth ($r = 0.989$), and the weakest was for HRTS 9 at 0.55 m depth ($r = 0.491$). At depth of 0.65 m, r values ranged between 0.583 (HRTS 10) and 0.707 (HRTS 8).

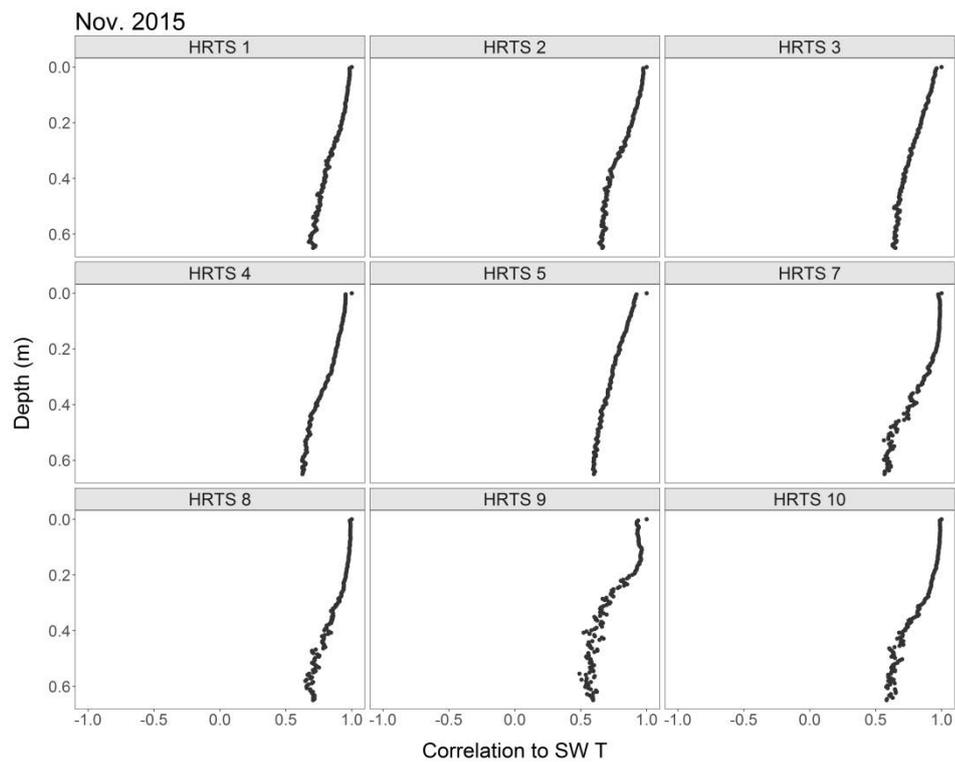


Figure 25. Significant correlation coefficients ($P < 0.01$) for each HRTS during 02-05/11/15.

In January (Figure 26), the strongest correlation was for HRTS 1 at 0.22 m depth ($r = 0.996$), and the weakest was for HRTS 10 at 0.65 m ($r = 0.655$). During January, correlations at 0.65 m depth in the streambed were on average the strongest (in absolute value) among all monitoring periods, ranging from 0.655 (HRTS 10) to 0.852 (HRTS 1).

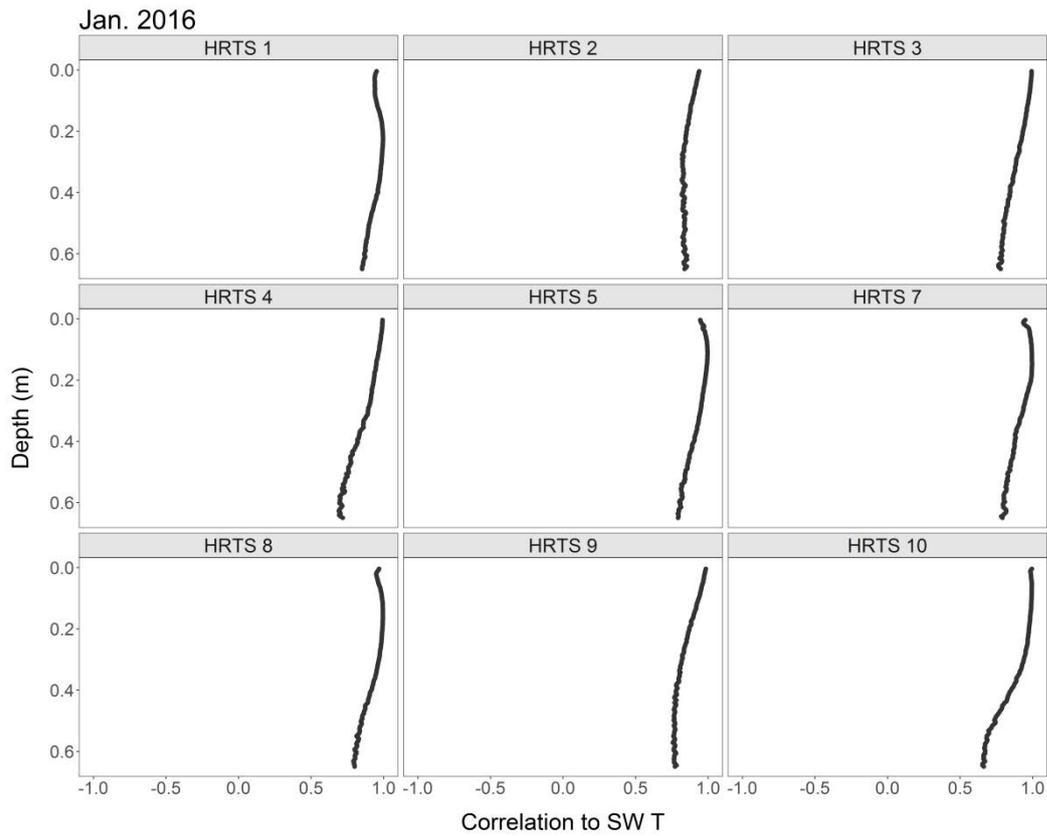


Figure 26. Significant correlation coefficients ($P < 0.01$) for each HRTS during 18-21/01/16.

5.3.4 LARGE WOOD INFLUENCE ON SEASONAL STREAMBED TEMPERATURES DYNAMICS

Streambed temperatures averaged over each entire monitoring period up to a depth of 0.65 m for all HRTS and with distinction between HRTS around woody structures (LWD) and those away from wood (no LWD) are summarized in Figure 27.

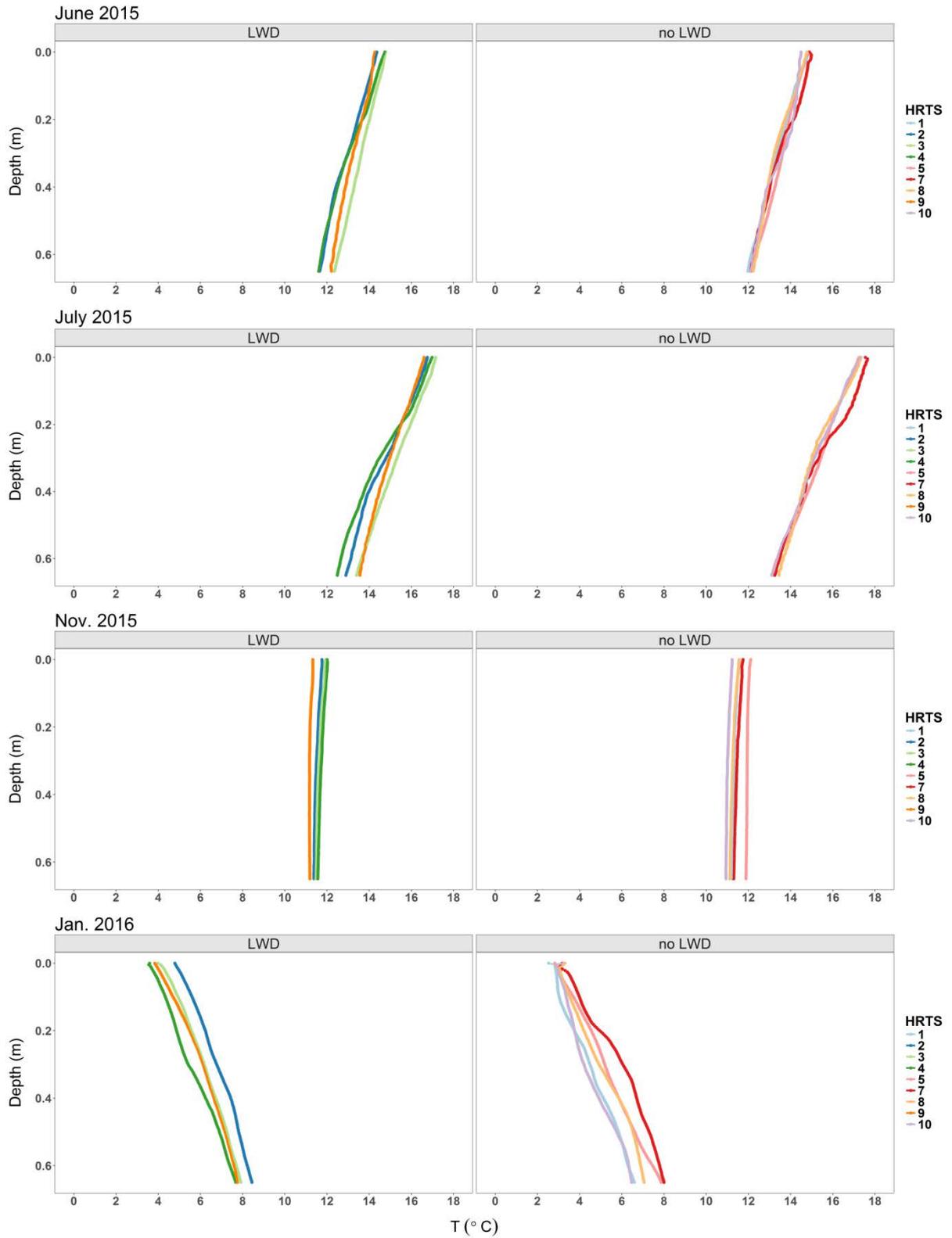


Figure 27. Streambed temperatures for each HRTS up to 0.65 m depth averaged over each monitoring period with distinction between locations around large wood (LWD) and locations away from LWD (no LWD).

HRTS exhibited similar mean thermal gradients over each monitoring period, and the proximity of large wood made no discernible differences in the general trends observed among HRTS during the same period, except in January. During the summer, the mean thermal gradients for all HRTS from warmer surface water-streambed interface to colder deep streambed sediments showed that surface temperature signal was transmitted through the streambed and was gradually attenuated with depth; during the autumn, the thermal gradients were almost linear, denoting similar thermal conditions between shallow and deeper sediments; during the winter, the thermal gradients observed during the summer reversed.

Spatio-temporal means of streambed temperatures varied with monitoring period ($P < 0.0001$), while the proximity/non-proximity to wood influenced spatio-temporal means of streambed temperature differently among monitoring periods (interaction factor, $P = 0.0002$). The proximity of large wood had a significant warming effect on spatio-temporal means of streambed temperatures around the LWD during monitoring period in January only ($P = 0.0018$; spatio-temporal means for LWD = 6.2 °C vs. no LWD = 5.1 °C), while the proximity to wood had no significant effect on spatio-temporal means of streambed temperatures during other monitoring periods (Table 18).

Table 18. Linear mixed effect model (LME) analysis results for spatio-temporal means of streambed temperatures associated with proximity/non-proximity to large wood, the monitoring period and the interaction between these factors.

Dependent variable	Factor	<i>d.f.</i>	<i>F</i>-value	<i>P</i>-value
Spatio-temporal means of streambed temperatures	Proximity/non-proximity to large wood (LWD/no LWD)	1	1.254	0.2997
	Monitoring period	3	1712.947	<0.0001
	Monitoring period x LWD/no LWD	3	10.711	0.0002

5.4 DISCUSSION

5.4.1. HYDROCLIMATOLOGICAL CONTROLS ON CHANGES IN STREAMBED SEDIMENTS TEMPERATURE DISTRIBUTIONS

Streambed temperatures patterns at the experimental site exhibited a number of important characteristics.

First, streambed temperatures exhibited clear and distinct seasonal spatio-temporal patterns, repeated similarly at all locations during each season, although with different magnitude. This was caused by seasonal variations in atmospheric heating and hydrological conditions, confirming the first hypothesis. The fact that during monitoring periods in the summer the upper limit of streambed temperature range of shallow sediments was higher than surface water - due to lower heat capacity of sediments relative to water - highlighted the significance of localized hydroclimatological conditions in driving spatio-temporal heterogeneity in streambed temperatures at the study site.

Second, in the summer at all locations streambed temperatures at shallow depths were higher than deeper sediments; during the winter, streambed temperatures increased with depth. Thus, also the second hypothesis that streambed temperature patterns observed during the summer would reverse during the winter was confirmed. These results are in agreement with findings of previous studies (Brunke & Gonser, 1997; Hannah, Malcolm & Bradley, 2009; Krause *et al.*, 2011a). In the summer, during day-time pulses of heated water were propagated from the surface into the subsurface by conduction and advection, while there was a progressive attenuation of surface temperature signal with depth, as indicated by the marked depth-related gradients found. The heat plumes that entered the subsurface during the day dissipated

overnight, thus the net result was the formation of diel temperature cycles in the shallow streambed sediments. In contrast, at greater depths streambed sediments were buffered and were not influenced by surface water temperature as shown by the correlation coefficients between streambed and surface water temperatures, and especially during July. Downward surface water infiltration increased with increasing water level in the autumn. In November, the homogeneous thermal patterns observed at all locations before the onset of the storm together with the strong and positive correlations between streambed and surface water temperatures at all depths indicated that most probably surface water penetrated deeply into the streambed sediments; this was a transition period during which streambed temperatures mirrored surface water thermal signatures. Increase of surface water contributions into the subsurface during periods of higher flow was previously found in other studies (Malcolm, Soulsby & Youngson, 2006; Hucks Sawyer *et al.*, 2009; Zimmer & Lautz, 2014). With the onset of the storm, surface water seemed to infiltrate at HRTS 2 and to converge towards HRTS 5 at the end of the meander, along a preferential flow path. Hyporheic exchange flow at these locations (HRTS 1-5) appeared to be enhanced by the top two woody structures and this is confirmed by the shorter residence times in shallow sediments in the vicinity of woody structures observed at the same study site by Shelley *et al.* (2017). The spatial difference in the response of streambed temperatures between HRTS in close proximity to woody structures and those farthest away was likely driven by wood-induced differential roughness of the bed morphology combined with channel sinuosity. However, this increased hyporheic exchange was not observed at the most downstream woody structure. Because the study site was completely flooded during the storm it was necessary to stop the DTS unit to prevent equipment damage, thus the full effects of the storm event were not detected. During the winter, the thermal gradients observed during the summer reversed and the relative higher and

more stable temperatures observed in the deep sediments buffered the cooling effect of winter prevailing meteorological conditions.

Under neutral hydrological conditions heat conduction in streambed sediments accounts for temperature variations at 20-cm depth of no greater than 10-15% of the amplitude of the surface water fluctuations (Silliman, Ramirez & McCabe, 1995), suggesting that temperature fluctuations of larger magnitude must be attributed to surface water advection (Storey *et al.*, 2003). Similarly, Krause *et al.* (2011a) calculated that a diurnal temperature oscillation of 2.5°C of the surface water would produce for thermal diffusivity values of sandy and gravelly sediments, in case of pure conduction, an average oscillation of 0.24°C at 0.40 m. A 2.5 °C-DTR for surface water was observed at the site on 18/06/15: at 0.40 m depth temperature oscillations on this day ranged from 0.7°C (HRTS 8) to 1.3°C (HRTS 10), beyond the limit of pure conduction only, and streambed temperature variation at 20-cm depth ranged from a minimum of 31% of the amplitude of surface water signal (HRTS 2) to a maximum value of 100% (HRTS 10). In summary, conduction and surface water advection were the main heat transfer mechanisms in the streambed at the study site.

5.4.2 THE POTENTIAL EFFECT OF LARGE WOOD ON STREAMBED TEMPERATURE PATTERNS

Large wood is known to increase subsurface thermal heterogeneity by inducing downwelling upstream woody structures and upwelling downstream (Kasahara & Hill, 2006; Sawyer *et al.*, 2011). This was observed during monitoring period in June when enough of the flowing stream's flow was blocked upstream the second top woody structure to increase the hydraulic head at HRTS 3 and drive subsurface exchange; during monitoring period in July this pattern was no longer evident to due dramatically reduced stream stage and flow velocity.

Yet, the effect of large wood on the whole mean thermal streambed conditions (from WSI to deep sediments) was only notable in January, during high flow discharge. In January in fact, the potential wood-induced increased hyporheic exchange flow resulted in warmer mean streambed temperatures at locations in close proximity to the woody structures, while mean streambed temperatures at locations farthest away were ~ 1 °C colder. This result could indicate that in lowland sand dominated streams considerable surface water velocities (e.g. high stream stage) are likely necessary to have significant enhanced hyporheic exchange around wood-induced bedforms able to impact on global mean streambed thermal conditions. In agreement with Daniels & Rhoads (2004), the spatial extent of LWD effects appears to increase with increasing stream stage.

5.5 CONCLUSIONS

Previous studies indicate that possible increases in the frequency and intensity of droughts due to climate change are expected to result in an increased temporal deterioration of water quality (van Vliet & Zwolsman, 2008). In fact, prolonged low-flow conditions in combination with high air temperatures can result in increased stream temperatures (e.g. Kaushal *et al.*, 2010; Orr *et al.*, 2015). The exchange of water between surface and ground water through the hyporheic zone is an important mechanism for the regulation of stream and streambed temperatures (Brookfield & Sudicky, 2012), as it creates unique and beneficial conditions that facilitate stream temperature buffering, while allowing aquatic invertebrates to avoid extreme temperatures or desiccation (Wood *et al.*, 2010). Therefore, a detailed understanding of the impact of droughts on water quality is essential to provide a robust basis for mitigation and restoration projects.

This research investigated variability in streambed temperature pattern distributions of a low land sand-dominated stream in the UK. Using high-resolution fibre-optic distributed temperature sensing, streambed temperatures were explored at nine locations, some of which in close proximity to large woody debris structures, across four sampling seasons (e.g. early summer, summer low-flow conditions, autumn and winter). Results indicated that streambed temperatures were variable in both space and time, with warming/cooling patterns primarily driven by seasonal hydroclimatological conditions. During summer low-flow conditions, streambed temperatures at shallow depths were particularly responsive to increased air temperature and localized very shallow water level. Groundwater contributions were excluded due to the presence of peat layers at shallow depths in the streambed, and the main heat transfer mechanisms were conduction and surface water advection. In winter, when stream discharge was high, mean streambed temperatures at locations around woody structures were on average higher than streambed temperatures at locations farthest away from large wood, and this is most likely due to wood-induced enhanced hyporheic exchange flow under high flow conditions.

5.6 SUMMARY

The use of high-resolution temperature sensors previously presented in Chapter 3 and 4 was tested in a real stream reach in the UK to determine at high spatio-temporal resolution seasonal changes in streambed temperatures at varying hydroclimatological conditions. The variability of streambed temperature patterns at the study site reflected hydroclimatological controls on stream and streambed temperatures, but also that spatial and temporal heterogeneity was driven by more local hydrological, morphological and sedimentary factors

(e.g. woody structures). The high-resolution temperature records detected the full spectrum of streambed temperature with depth through time, thus the use of fibre-optic distributed temperature sensors revealed to be a promising approach for investigating seasonal variations of streambed temperatures.

CHAPTER 6: SYNTHESIS AND FUTURE DIRECTIONS

6.1 INTRODUCTION

The research presented in this thesis was motivated by substantial evidence of the impacts of drought on freshwater ecosystems induced by climate change (Rosenzweig *et al.*, 2007; Whitehead *et al.*, 2009; Leigh *et al.*, 2015), and by the fact that further changes are projected. The frequency of extreme events like intense precipitation, heatwaves and droughts have and will continue to increase (Easterling *et al.*, 2000; Kundzewicz *et al.*, 2008; Coumou & Rahmstorf, 2012). In particular, projected decreases in low flows will exacerbate the sensitivity of hydrological and thermal regimes of rivers to increased atmospheric energy input, with direct consequences for freshwater ecosystems, water quality and human water use (Bond *et al.*, 2008; van Vliet *et al.*, 2013). The understanding of the impacts of the predicted drought severity and frequency on water quality is currently still uncertain, and this knowledge gap results to a large degree from limitations in current sensing technologies that are not able to adequately represent the complex water thermal regimes and process of interconnected groundwater-surface water systems (Fleckenstein *et al.*, 2010; Krause *et al.*, 2013). Through the application of FO-DTS technology and in particular using fibre-optic high resolution temperature sensors (HRTS), the research yielded new knowledge on the sensitivity of freshwater ecosystems to drought and potential resistance/resilience to a warming climate.

The thesis adopted a multi-scale research design and addressed four research objectives in four interlinked chapters. In Chapter 2 (objective 1), the combined effect of drought-induced water level variation and co-evolved vegetation coverage on streambed and surface temperature patterns of artificial rivers were quantified using FO-DTS. In Chapter 3 (objective 2), HRTS were used to quantify thermal stress in gravel streambeds of laboratory

mesocosms following altered groundwater-surface water exchange and increased surface water temperatures. In Chapter 4 (objective 3), the experimental approach adopted in Chapter 3 was further developed to test the hyporheic refuge hypothesis under different groundwater-surface water exchange and warming scenarios. In Chapter 5 (objective 4), HRTS were used in a real stream reach to quantify seasonal variability in streambed sediments temperature distributions in a forested stream in the UK. In this concluding chapter, the key research findings are summarised and synthesized, and recommendations for further research proposed.

6.2 KEY RESEARCH FINDINGS

The major outcomes of the research were as follows:

1. Thermal dynamics in co-evolved vegetated flumes with varying water depths were characterized by high spatial heterogeneity. Water levels, together with aquatic vegetation via shading, controlled the sensitivity of the flume temperature regimes to changes in air temperature and solar radiation receipt. Quantification of warmings during simulated low flows demonstrated the importance of maintaining minimum water level conditions that can buffer temperature extremes and increase thermal heterogeneity in lowland streams during drought.
2. The direction of groundwater-surface water exchange impacted on the transfer of thermal stress into gravel streambeds under different warming scenarios. While surface water signal was highly attenuated at shallow depths under upwelling conditions owing to upward advection of cooler water, heat was transmitted up to considerable depths in the streambed sediments under downwelling conditions, due to combined conductive-advective downward heat transport. Consequently, the

sensitivity of streambed thermal regime to increased surface water temperature was higher under downwelling conditions, with shallow sediments being especially affected.

3. Alteration of the direction of groundwater-surface water exchange influenced the potential of the hyporheic zone of gravel streambeds to provide a refuge for *Gammarus pulex* under warming. With increasing surface water temperature, leaf-litter breakdown was observed at a greater depth under downwelling conditions, suggesting that organisms migrated deeply with the flow into the hyporheic zone to escape high surface temperature. In contrast, upwelling flows seemed to constrain habitat availability to the shallow sediments, decreasing organismal survival rates. Surprisingly, surface water temperature did not affect survival rates only the direction of groundwater-surface water exchange did, indicating that saturated gravel streambeds in which surface water and groundwater can mix have the potential to increase resilience of riverine communities under a warming climate as surface water temperature extremes in the hyporheic sediments were highly buffered.
4. Seasonal variations of streambed temperatures in a forested stream reach are primarily driven by hydroclimatological conditions. At summer low-flow conditions, when water velocity was reduced, shallow sediments were particularly impacted by conductive-advective downward heat transport, while in the deeper sediments surface temperature signal was attenuated. During autumn, streambed thermal regimes were reset, and in winter, streambed temperature patterns observed were the reversed of summer conditions with temperature increasing with depth. Despite the exclusion of groundwater contributions, hyporheic exchange flow between surface and more

deeply water due to large woody structures increased the heterogeneity of streambed temperatures at locations around wood.

6.3 SYNTHESIS

This section synthesises the new knowledge yielded in the thesis to assess the impacts of drought on thermal and water extremes.

Temperature is an important characteristic of rivers, affecting water quality and overall health of aquatic ecosystems (Caissie, 2006; Webb & Nobilis, 2007). Stream temperature is dependent on both heat load and stream discharge, thus any process that influences heat energy or discharge in the channel will influence water temperature (Poole & Berman, 2001). Due to climate change, hydrological and thermal regimes of rivers are expected to change (van Vliet *et al.*, 2013). Combined effects of atmospheric warming and changes in river flow - for example due to water withdrawals - significantly impact water temperatures, and particularly during warm, dry periods with low flows when water temperatures are most sensitive to atmospheric influences and can reach critical high values (van Vliet *et al.*, 2011).

The research presented in this thesis shows that low-flow conditions control stream thermal dynamics (Chapter 2). Stream shallower water areas, and especially features where bed sediments are dry and aquatic vegetation sparse (e.g. riffles), are expected to show greater spatial and temporal temperature heterogeneity in water temperature, thus quicker and stronger responses to different meteorological conditions compared to channel areas where water is deeper (e.g. pools). Aquatic vegetation like submerged macrophytes, coevolving with different water depths in the channel, can contribute to reduce temperature extremes in both surface water and at the water-sediment interface, buffering day-time energy receipt via

shading, and reducing evaporative losses at night time. In natural riverine ecosystems, geomorphic features like riffles and steps, and biological features like macrophytes aggregations and downed wood, add flow roughness to drive hydrological exchange processes between shallow groundwater and surface water through the hyporheic zone (Harvey, 2016). These exchanges of water are important for the regulation of stream and streambed temperatures (Brookfield & Sudicky, 2012). During warming, in saturated gravel streambeds in which vertical exchange flows occur, thermal stress is controlled by the direction of ground water-surface water exchange (Chapter 3), with upwelling areas being less sensitive to increased surface water temperatures compared to downwelling zones. Upwelling of cool water during warming ensures more stable temperature and reduces temperature range in the hyporheic sediments. Furthermore, under warming, the direction of groundwater-surface water exchange affects the hyporheic refuge capacity of gravel streambeds (Chapter 4). High surface water temperatures trigger *Gammarus pulex* to actively migrate into the hyporheic zone to seek for refuge. Downwelling flow conditions prompt to better promote organismal survival than upwelling flows (Folegot *et al.*, 2018). The volume of habitat availability is in fact contracted and constrained to the shallower sediments where higher temperatures are present under upwelling flows. Localized crowding can intensify biotic interactions as well as competition for food resources and space (Covich, Crowl & Scatena, 2003). Downwelling flows can instead facilitate the downward migration of organisms with the flow direction (Stubbington *et al.*, 2011), increasing the resilience of riverine communities to drought-induced warming.

Variations in hydroclimatological conditions determine seasonal variations of streambed temperatures of a forested low-land stream (Chapter 5). Seasonal changes in air temperature and water level conditions primarily control spatial and temporal variability of streambed temperature patterns. During summer low-flow conditions, streambed temperatures at shallow depths are particularly responsive to increased air temperature and localized very shallow water level, and

temperature decreases with increasing depth. In winter, when stream discharge is high, streambed temperature patterns are reversed, with temperature increasing with depth. The use of high-resolution temperature sensors can provide valuable, high-resolution observations of complex and variable patterns of streambed temperatures.

6.4 IMPLICATIONS AND FURTHER RESEARCH AVENUES

Research herein suggests that an ecosystem-based management needs to be adopted to enhance the resilience of rivers and to minimize the impacts of drought. The effects of multiple environmental stressors on riverine ecosystems will likely intensify the negative impacts of climate change (Palmer *et al.*, 2009), therefore identifying accommodation and adaptation strategies is the first priority river and water managers should consider.

The depletion of flow by excessive extractions of river water or groundwater during low-flow periods is one of the major threat to ecological sustainability of rivers (Bunn & Arthington, 2002), causing alterations of their thermal regime (Caissie, 2006). The thermal capacity of a stream is reduced when discharge is reduced (Poole & Berman, 2001; Webb *et al.*, 2003), thus greater temperature variations are expected in shallower water areas (Chapter 2) or during summer low-flows (Chapter 5). In addition, variations in water depth, discharge and velocity directly affect aquatic vegetation by altering the composition and abundance of aquatic macrophyte communities (Riis & Biggs, 2003). In lowland streams, longer and more severe periods of low flow will cause shifts between aquatic and opportunistic amphibian/terrestrial plant species (Wassens *et al.*, 2017) which are characterized by different shading abilities. Shading by dense macrophytes mats like *Ranunculus* spp. can significantly reduce radiative inputs (Clark *et al.*, 1999), buffering water temperature below the vegetation (Chapter 2).

Consequently, appropriate environmental flow management should involve restricting abstraction, to achieve an altered flow regime that still sustains robust, persistent aquatic plant community, and maintains highly diversified thermal habitat conditions in a flexible and adaptive management framework under shifting hydro-climatic and ecological conditions (Poff, 2017).

The other approach the results of this research suggest is to increase riverine ecosystems resilience by identifying the location, spatial extent and physical properties of potential refuges in which species can retreat, allowing them to persist under drought-induced critical temperatures. The hyporheic zone of saturated gravel streambeds has the potential to provide a refuge to some benthic organisms like *Gammarus pulex* from increased surface water temperature (Chapter 4). However, the direction of groundwater-surface water exchange plays a fundamental role in controlling thermal stress into the streambed sediments (Chapter 3) and affecting organismal survival (Chapter 4). And, the effectiveness of the hyporheic refuge capacity might be at risk when the vertical hydrological connectivity between stream and surrounding near stream subsurface water is altered (e.g. shifts between up- and downwelling flows, channel modifications that reduce hydro-geomorphological heterogeneity) or completely lost (e.g. fines clogging streambed sediments, lowered groundwater table). On one hand, upwelling flows sustain surface water with colder groundwater discharge to the stream, buffering thermal stress in streambed sediments and maintaining base flow conditions (Brunke & Gonser, 1997; Caissie, 2006; Miller *et al.*, 2016); on the other, downwelling water may facilitate initial refuge use (Stubbington, 2012) and promote subsequent benthic recolonization. There is strong evidence to suggest that downwelling flows, and particularly when local downwellings are nested in a major downwelling (Maazouzi *et al.*, 2017), have the potential to act as a refuge during drying (Maazouzi *et al.*, 2017) or surface water warming

(Folegot *et al.*, 2018). Although a comprehensive understanding of determinants and mechanisms of hyporheic refuges is still not complete, all this highlights the importance of maintaining vertical connectivity during and after disturbance events like droughts (Boulton, 2007). The hyporheic zone requires protection (Stubbington, 2012), and typical rehabilitation schemes should focus on the manipulation of riverbed sediments by adding gravel to create sedimentary refuges (Barlaup *et al.*, 2008), reintroducing woody debris and creating riffle-pool sequences to promote vertical hydrological exchange (Kasahara & Hill, 2006; Mutz *et al.*, 2007; Kasahara *et al.*, 2009; Boulton *et al.*, 2010), flashing sediments to remove clogging and sustain sediment permeability (Kasahara *et al.*, 2009).

Further extending the contemporary understanding of the impacts of drought on thermal and water extremes may increase the success of rehabilitation schemes. To achieve this, future research should seek to address the following research gaps:

- Work presented herein has yielded knowledge on the impacts of low flows on stream thermal dynamics (Chapter 2). However, more research would need to be carried out to separate the single impacts of different vegetation coverage from different water depths on lowland stream thermal regimes, and FO-DTS technology may provide an effective high frequency, high resolution spatial and temporal monitoring tool;
- Although *Gammarus pulex* belongs to a key trophic guild in stream ecosystems (Boyero *et al.*, 2012) and is an appropriate model organism to study climate change effects on freshwater ecosystems, the potential of hyporheic sediments to effectively provide a refuge from drought and warming conditions needs to be tested also for different taxa, and possibly using a heterogeneous sediment matrix. The volume of hyporheic refuges varies indeed with substrate composition (Stubbington, 2012), with coarse sediments supporting more diverse, high density communities (Strayer *et al.*,

1997). This information is crucial to assess the real importance of the HZ in benthic resilience under a changing climate.

- Further insight to the influence of varying hydroclimatological conditions on seasonal streambed temperatures of lowland forested streams might be obtained from a longer term data collection. Longer term spatially distributed temperature data collected with HRTS throughout each season may be particularly useful to inform 1-D numerical models (e.g. VFLUX, Gordon *et al.*, 2012) to better understand highly dynamic surface and sub-surface water interactions.

6.5 FINAL REMARKS

The research presented in this thesis has provided a framework to improve our understanding of the risk of low flows, surface warming, shifts between up- and downwelling flows, and hydroclimatological controls on streambed temperature dynamics and associated functions at a number of spatial and temporal scales. As such, it contributes significant new knowledge that may be used by river and water managers in decision making regarding lowland streams and HZ-specific rehabilitation strategy to increase riverine resilience to temperature and water extremes.

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APPENDIX: PEER REVIEWED ARTICLES
ACCEPTED FOR PUBLICATION

Folegot S, Hannah DM., Dugdale SJ, Kurz MJ, Drummond JD, Klaar MJ, Lee-Cullin J, Keller T, Martí E, Zarnetske JP, Ward AS, Krause S, in press. Low flow controls on stream thermal dynamics, *Limnologica - Ecology and Management of Inland Waters*. DOI: 10.1016/j.limno.2017.08.003.

Folegot S, Krause S, Mons R, Hannah DM, Datry T, 2018. Mesocosm experiments reveal the direction of groundwater–surface water exchange alters the hyporheic refuge capacity under warming scenarios, *Freshwater Biology*. DOI: 10.1111/fwb.13049.