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Macroinvertebrate and diatom community responses to thermal alterations below water supply reservoirs

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Abstract

River impoundments have transformed river ecosystems globally due to the modification of various abiotic and biotic factors. This study provides rare evidence quantifying how water supply reservoirs alter water temperature regimes and its effects on macroinvertebrate and diatom communities over a 4-year period. We obtained near-continuous water temperature measurements upstream and downstream of three reservoirs and analysed thermal variables in association with macroinvertebrate and diatom community indices (including taxonomic richness, proportion of Ephemeroptera, Plecoptera and Trichoptera taxa [%EPT] and diatom ecological guilds). Reservoirs typically decreased downstream thermal variability, with reduced summer temperatures and increased winter temperatures, and a delayed timing of annual temperature extremes. Marked differences in thermal regime modifications between reservoirs were observed, including evidence of inter-annual variation associated with inter-basin water transfers downstream of one reservoir. Biomonitoring indices showed associations with thermal indices that differed between site types (regulated versus non-regulated) and seasons (spring vs. autumn). Various macroinvertebrate and diatom indices capturing community diversity elements and sensitivities to different environmental pressures were associated with higher maximum summer temperatures and lower minimum winter temperatures, suggesting ecological effects of reduced thermal variation downstream of reservoirs. Different ecological responses to thermal indices were observed between seasons, likely due to organism life-cycle effects and intra-annual thermal variations. Contrasting macroinvertebrate and diatom communities were observed between regulated and non-regulated sites, which may be driven by differences in the thermal regime and other abiotic factors at regulated sites, including nutrient, sediment and flow regimes. Long-term continuous water temperature monitoring of both multiple regulated and non-regulated river systems is necessary to better understand the environmental and ecological effects of river impoundments. Given the extent to which river impoundment has modified stream temperatures globally, the inclusion of thermal regime data in environmental flow studies alongside hydrological information may guide the implementation of mitigation measures on impounded waterbodies.

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KEYWORDS

benthic diatoms, macroinvertebrates, regional-scale analysis, river regulation, thermal alterations, water supply reservoirs

1 | INTRODUCTION

The construction of dams and reservoirs, collectively referred to as river impoundments, represents one of the primary anthropogenic activities transforming riverine environments globally (Grill et al., 2019; Malmqvist & Rundle, 2002). In recent decades, a large body of evidence has demonstrated how impoundments have modified different abiotic regimes (e.g., Arora et al., 2017; Ellis & Jones, 2013; Petts, 1984; Wang, Maberly, Wang, & Liang, 2018). The majority of studies exploring ecological responses to modified abiotic conditions in regulated rivers have focused on geomorphological (Greenwood, Bickerton, Gurnell, & Petts, 1999) and, more recently, flow modifications (e.g., Magilligan & Nislow, 2005; Maynard & Lane, 2012; Poff & Zimmerman, 2010; White et al., 2017). By influencing all components of the natural flow regime (*sensu* Poff et al., 1997), river impoundment can have significant effects on riverine communities in regulated rivers, modifying flow–ecology relationships (Bunn & Arthington, 2002; Chen & Olden, 2018; Ruhi, Dong, McDaniel, Batzer, & Sabo, 2018). In addition to river flow regimes, water temperature is acknowledged to play a vital role in influencing the ecology of riverine ecosystems (Caissie, 2006; González-Tokman et al., 2020; Ward & Stanford, 1982). The components of the natural thermal regime (*sensu* Olden & Naiman, 2010) are important drivers of life-histories of many aquatic organisms, such as thermal cues triggering spawning, migratory activities, or metamorphosis (Beer & Steel, 2018; Nordlie & Arthur, 1981).

The presence of a reservoir can severely modify the thermal regime of the river downstream, including increasing winter water temperatures (Dickson, Carrivick, & Brown, 2012; Raddum, 1985), reducing summer temperatures (Soja & Wiejaczka, 2014; Vinson, 2001), increasing diel constancy (Casado, Hannah, Peiry, & Campo, 2013; Horne, Rutherford, & Wehrly, 2004), and changing the timing of thermal events (Cowx, Young, & Booth, 1987; Preece & Jones, 2002). Thermal alterations within regulated rivers have been shown to prompt a range of ecological responses, including behavioural changes (Catenazzi & Kupferberg, 2018), demographic shifts (e.g., birth rate, recruitment—Rolls et al., 2013), the composition and diversity of biotic communities (Benítez-Mora & Camargo, 2014; Lessard & Hayes, 2003), ecosystem functionality (Bruno et al., 2019; White et al., 2017), and food-web complexity (Cross et al., 2013).

Although research on the ecological effects of impoundments has often identified thermal changes as one of the primary drivers of community changes (e.g., Raddum, 1985; Stevens, Shannon, & Blinn, 1997), few studies have directly quantified the effect using water temperature measurements. Those studies that have considered thermal changes below reservoirs have usually focused on fish communities or target species within these (e.g., Horne et al., 2004; Maheu, St-Hilaire,

Caissie, & El-Jabi, 2016) or, to a lesser extent, on macroinvertebrate communities (e.g., Jackson, Gibbins, & Soulsby, 2007; Phillips, Pollock, Bowman, McMaster, & Chivers, 2015; Raddum, 1985). Studies considering other ecological groups, for example benthic diatoms, are rare (but see Blinn, Truitt, & Pickart, 1989; Grown & Grown, 2001). The burgeoning literature on environmental flows or e-flows (Poff & Matthews, 2013) has typically focused on introducing more natural flow regime elements downstream of reservoirs to sustain lotic ecosystems in regulated rivers (Acreman et al., 2009; Arthington, 2012). However, restoring near-natural flow regimes is often not feasible in heavily modified river systems. Instead, emerging concepts like ‘designer flows’ (Chen & Olden, 2017; Tonkin et al., 2021) and ‘functional flows’ (Yarnell et al., 2015, 2020) consider conveying specific hydrological events through the channel that are ecologically beneficial, whilst also delivering societal needs (see also Acreman et al., 2014). However, there is a general absence of long-term, continuous water temperature measurements, and thermal regimes are rarely acknowledged or included in e-flow studies (Olden & Naiman, 2010). This would require temperature–ecology relationships to be established beyond the scale of individual reservoirs. In line with observations for flow–ecology relationships (see for example Bruckerhoff, Leasure, & Magoulick, 2019; Poff & Zimmerman, 2010), large-scale temperature–ecology relationships are likely to be elusive for different reasons, such as biogeographical variations in local species pools that respond differently to thermal controls, as well as changes in environmental controls across regional (e.g., flow regimes) and local scales (e.g., hyporheic zone refugia).

In this paper, we examined water temperature regimes upstream (non-regulated) and downstream (regulated) of three water supply reservoirs and their influences on macroinvertebrate and diatom community indices. Our overarching research objective was to examine differences between thermal regimes upstream (i.e., non-regulated) and downstream (i.e., regulated) of water supply reservoirs and the implications this has for instream communities. We addressed the following two research questions in relation to the three reservoirs: (a) How do water supply reservoirs modify thermal regimes and are these changes consistent across reservoir sites? (b) How do macroinvertebrate and diatom communities respond to antecedent water temperature conditions in regulated and non-regulated systems?

2 | METHODOLOGY

2.1 | Reservoir data

We undertook this study at three water supply reservoirs that are located in upland areas in England, UK: Winscar, Ladybower and

Derwent reservoirs. All three reservoirs have established upstream (non-regulated, above the reservoir) and downstream (regulated, below the dam) biological monitoring sites. Winscar and Ladybower reservoirs are situated in the Peak District (Figure 1). Winscar Reservoir, impounding the River Don, has a surface area of 0.51 km^2 and impounds $c 9 \cdot 10^6 \text{ m}^3$, with an average depth of 18 m (max 42 m). Ladybower Reservoir, impounding the rivers Derwent (Derbyshire, UK) and Ashop, covers 2 km^2 and impounds $c 28 \cdot 10^6 \text{ m}^3$, with an average depth of 29 m (max 41 m). A predominantly fixed compensation flow regime ('compensation flows'—Gustard, 1989) is in place downstream of both reservoirs, but the discharge can vary due to spilling during periods of high precipitation and high water levels. The compensation flow downstream of Ladybower reservoir is 57 ML/d throughout the year (Maddock, Bickerton, Spence, & Pickering, 2001). For Winscar reservoir, compensation flows ($c 10 \text{ ML/d}$) are predominantly delivered from two neighbouring reservoirs, entering the river below the downstream sample site, but can be released from Winscar Reservoir as well.

The third study site, Derwent Reservoir, is situated on the River Derwent in Northumberland in North East England (Figure 1). The

reservoir has a surface area of 4 km^2 and impounds $c 50 \cdot 10^6 \text{ m}^3$, with a maximum depth of $c 30 \text{ m}$. Compensation flows range between 22.7 and 25 ML/d (Maynard & Lane, 2012), which are released from either the reservoir itself or via the Kielder Water transfer from the regulated River Tyne (Soulsby et al., 1999). The timing and duration of the water transfer vary between years, depending on meteorological conditions and reservoir water levels. No thermal de-stratification measures are in place at any of the reservoirs. For Winscar and Ladybower Reservoir, one downstream (regulated) site and one upstream (non-regulated) site closest to the reservoir were selected for detailed investigation. For Derwent Reservoir, two downstream sites and one upstream site were selected, resulting in a total of seven sample sites for the three reservoirs.

2.2 | Temperature data

Sub-aquatic Gemini Tinytag Aquatic 2 temperature sensors were installed at the sample sites upstream and downstream of Ladybower and Winscar Reservoirs to record water temperatures at 1-hour

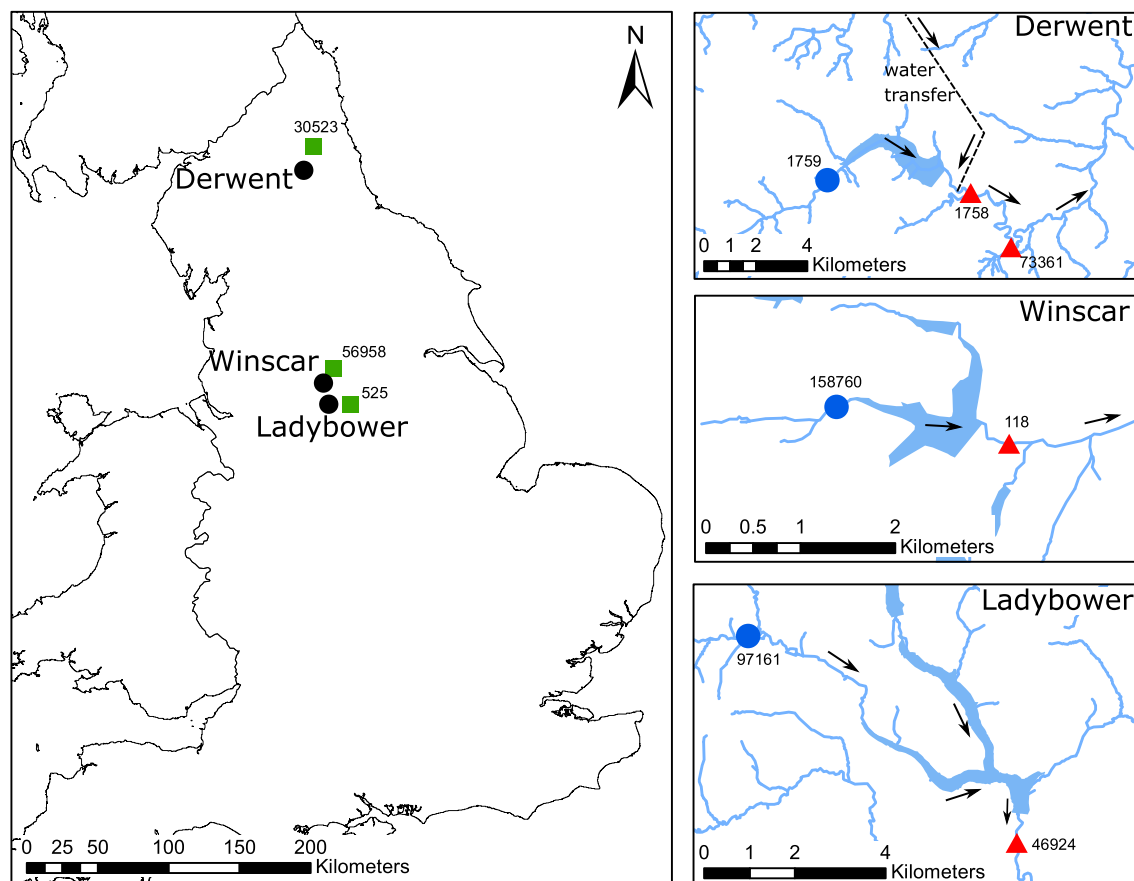


FIGURE 1 Location of the three reservoirs, accompanying sample sites, and air temperature stations used in the thermal alteration study. Blue circle = upstream (non-regulated) site; Red triangle = downstream (regulated) site; green square = air temperature station. The labels at the sample sites and temperature stations indicate the site ID. Arrows indicate flow direction. The approximate course of the Kielder water transfer is indicated with the dashed line (see Soulsby, Gibbins, & Robins (1999) for more information on the water transfer scheme) [Color figure can be viewed at wileyonlinelibrary.com]

intervals. To minimise the chance of data loss and to provide replication to confirm readings, two sensors were installed at each site. All sensors were installed from May–June 2017 to June 2018. Sensors were placed in deeper parts of the channel (> 30 cm to ensure submergence) in marginal areas shaded by riparian vegetation or rocks to prevent direct exposure to sunlight (see Johnson & Wilby, 2013). The measurements upstream and downstream of Derwent Reservoir were collected by the Environment Agency (the environmental regulator of England) using Tinytag Plus 2 sensors between November 2016–February 2019. In addition, hourly water temperature data for the River Tyne c 11 km upstream of the entry point of the Kielder Water transfer scheme was available for the period October 26, 2016–April 24, 2019.

Air temperature measurements from three meteorological stations were obtained through the Met Office Integrated Data Archive System (MIDAS—Met Office, 2012) for the period 2011–2019. Stations were selected based on proximity to study sites and data series completeness and were all located within 25 km of the paired reservoirs (Figure 1).

2.3 | Ecological sampling and biomonitoring indices

At all seven sites, macroinvertebrate and diatom communities were sampled biannually during spring (March–May) and autumn (September–November) between 2013 and 2016. These years had average to above-average annual rainfall, with no prolonged dry periods (Met Office, 2019). Benthic macroinvertebrates were collected using the standard Environment Agency sampling methodology. Sample sites were focused on riffle habitats and the river sampled, so that the proportion of each habitat was sampled relative to its occurrence. Samples were collected by means of a standardised 3-min kick-sampling method with an additional 1-min hand search (Murray-Bligh, 1999) and subsequently preserved and processed following a standardised procedure (ISO, 2012). Macroinvertebrate taxa were identified to a consistent mixed taxonomic level (mainly to species level, but some taxa to genus- or family-level—Davy-Bowker et al., 2010), with total abundances being recorded. Pre-analysis quality assurance procedures were undertaken to ensure specimens across all samples were resolved to a consistent taxonomic resolution (Krajenbrink et al., 2019b). The total number of macroinvertebrate samples was 55 (27 spring and 28 autumn samples), with one missing spring sample downstream of Ladybower Reservoir. For every sample, total taxa richness (N_{taxa_MI}), the relative proportion of Ephemeroptera, Plecoptera and Trichoptera taxa per sample (%EPT) and the Walley–Hawkes–Paisley–Trigg index (WHPT; Paisley, Trigg, & Walley, 2014) were calculated. The total taxa richness (N_{taxa_MI}) was used to reflect the biodiversity of macroinvertebrate communities as it is widely used routinely in biomonitoring studies and has been found to respond directly to stream temperature regimes (e.g., Durance & Ormerod, 2007). Macroinvertebrate taxa belonging to the insect orders Ephemeroptera (mayflies), Plecoptera (stoneflies)

and Trichoptera (caddisflies) are widely used as indicators of river ecosystem health and have been widely used as indicators of changes to river flow regimes and ecosystem health (Mathers, Chadd, Extence, Rice, & Wood, 2016; Tonkin et al., 2015). The WHPT index, based on family-level macroinvertebrate data, was derived to assess the biological water quality/health of rivers by characterising community tolerance to nutrient enrichment.

Diatom sampling followed EA protocols (WFD-UKTAG, 2014) which conform to European standards for routine diatom sampling and preparation in rivers and lakes (CEN, 2014b). Diatom frustules were prepared on slides and subsequently identified by counting a minimum of 300 valves of benthic diatom taxa, comprising at least 200 valves of non-dominant taxa (CEN, 2014a). Diatom valves were identified to species level where possible, with taxa that formed < 2% of the sample typically being resolved to genus level. In addition, a pre-analysis quality assurance on taxonomy and nomenclature was carried out (for further details on diatom sampling and analysis procedures, see Krajenbrink et al., 2019a). The total number of diatom samples was 54 (27 spring and 27 autumn samples). For every sample, the total taxonomic richness of benthic diatom taxa (N_{taxa_D}) was determined. N_{taxa_D} was investigated in more detail by segregating all benthic taxa into three diatom ecological guilds based on growth morphologies and their ability to tolerate nutrient limitation and physical disturbance, that is, low-profile, high-profile and motile guilds (Passy, 2007). For every sample, the percentage of taxa belonging to each guild (relative richness – % $_{taxa_low}$; % $_{taxa_high}$; % $_{taxa_motile}$) was calculated. Each taxon was assigned to a guild using the diatom checklist from Rimet and Bouchez (2012). In addition, Trophic Diatom Index (TDI) scores were derived. The TDI methodology was initially developed to characterise ecological responses to nutrient enrichment (Kelly et al., 2008; Kelly & Whitton, 1995), but may also be useful to characterise the influence of other environmental controls associated with water quality and the flow regime. TDI scores (version TDI4, based on mixed taxonomic level, up to species level) were calculated by the EA following guidelines in WFD-UKTAG (2014).

2.4 | Data analysis

The analysis for this study comprised two separate steps. In step 1, the thermal regimes upstream and downstream of the reservoirs, as well as air temperature, were compared for a period of 1 year. For Winscar and Ladybower Reservoirs, the temperature analysis period was 1st June 2017–31st May 2018 (although measurements for the site upstream of Winscar Reservoir commenced late June 2017). The analysis period for Derwent Reservoir was 1st February 2017–31st January 2018. The slight shift in time was based on the operation regime of the Kielder Water transfer, which was in permanent use during this period, except for 1st–19th February 2017, 31st March–17th April 2017 and 26th–31st January 2018. To compare the non-regulated site upstream of Derwent Reservoir with the non-regulated sites upstream of Winscar and Ladybower Reservoirs, additional data for this site was extracted for the period 1st June 2017–31st May

2018. Raw 1-hr interval water temperature measurements were aggregated to average daily values. Subsequently, 28 thermal regime indices were calculated and compared between sites. Some of these indices were based on IHA parameters (*sensu* Richter, Baumgartner, Powell, & Braun, 1996) that we adapted for use in thermal regime analysis, representing all key components of the thermal regime (i.e., Magnitude, Duration, Timing, Frequency, and Rate-of-change), while other ecologically relevant thermal indices reflecting specific temperature magnitudes (e.g., T10—the temperature that is exceeded 10% of the time) were also incorporated (Olden & Naiman, 2010; White et al., 2017). A description of the indices and the assigned thermal regime components is presented in Table 1. In addition, monthly mean water temperatures of the River Tyne were compared with

monthly mean values upstream and downstream of Derwent Reservoir for the period November 2016–February 2019.

In step 2, macroinvertebrate and diatom community response metrics were analysed in association with thermal indices based on modelled antecedent water temperature time series. Since no water temperature measurements were taken during the biomonitoring period (2013–2016), Generalised Additive Models (GAM) were constructed between water and air temperature time series, following White et al. (2017), using the `gam` function from the R package `mgcv` (Wood, 2019). Air temperatures were modelled using thin-plate spline regression smoothers. To account for seasonality, week number was added as an extra smoothing parameter using a cyclic cubic spline smoother. For the sample sites upstream and downstream of Winscar

TABLE 1 Description and values of thermal indices

Variable	Regime component and description	Ladybower		Winscar		Derwent			
		NR	R	NR	R	NR_v1	NR_v2	R1	R2
T10	M Temperature (°C) equalled or exceeded 10% of the time	13.5	12.0	12.7	12.4	13.7	13.8	16.1	15.1
T30	M Temperature (°C) equalled or exceeded 30% of the time	11.4	10.4	10.7	10.9	11.8	11.7	14.2	13.0
T50	M Temperature (°C) equalled or exceeded 50% of the time	8.8	7.5	7.6	8.7	8.5	8.8	10.2	9.9
T70	M Temperature (°C) equalled or exceeded 70% of the time	5.2	5.2	4.5	5.1	3.9	5.5	6.1	5.8
T95	M Temperature (°C) equalled or exceeded 95% of the time	2.3	3.4	1.8	3.0	1.2	1.7	3.2	1.9
Jan_mean	M Mean January temperature (°C)	4.5	4.3	3.7	4.3	3.1	3.1	3.5	3.3
Feb_mean	M Mean February temperature (°C)	3.2	3.8	2.5	3.9	2.2	4.1	4.1	4.3
Mar_mean	M Mean March temperature (°C)	3.5	3.5	2.9	3.6	2.7	5.9	6.8	6.5
Apr_mean	M Mean April temperature (°C)	7.3	5.2	6.7	5.9	6.7	7.6	8.8	8.6
May_mean	M Mean May temperature (°C)	11.8	6.7	10.9	9.7	11.5	11.8	13.5	13.1
Jun_mean	M Mean June temperature (°C)	13.0	9.5	-	12.1	13.5	13.5	16.3	15.2
Jul_mean	M Mean July temperature (°C)	13.8	10.3	13.3	12.5	13.5	13.5	15.8	15.0
Aug_mean	M Mean August temperature (°C)	12.5	11.5	12.3	12.1	13.3	13.3	15.6	14.7
Sep_mean	M Mean September temperature (°C)	10.8	12.6	10.6	10.7	11.2	11.2	13.4	12.5
Oct_mean	M Mean October temperature (°C)	9.7	11.8	9.5	10.0	9.7	9.7	11.3	10.7
Nov_mean	M Mean November temperature (°C)	6.3	9.1	6.1	7.1	5.0	5.0	6.6	5.7
Dec_mean	M Mean December temperature (°C)	4.5	5.7	4.0	5.4	3.2	3.2	3.9	3.3
TMAX	M Maximum temperature (°C)	17.4	13.0	15.6	15.1	17.0	17.2	18.8	18.0
TMAX3	M Maximum 3-day average temperature (°C)	16.7	12.9	15.3	14.6	16.6	16.6	18.6	17.5
TMAX3JD	T Day-of-year of maximum 3-day average temperature	170	269	198	169	170	170	173	170
TMIN	M Minimum temperature (°C)	-0.1	3.0	-0.1	2.2	-0.1	0.0	2.1	0.4
TMIN3	M Minimum 3-day average temperature (°C)	0.0	3.1	0.0	2.5	-0.1	0.6	2.2	1.1
TMIN3JD	T Day-of-year of minimum 3-day average temperature	60	71	60	77	61	345	349	345
THPC	F High-pulse count (events > T25)	11	1	11	11	14	12	4	10
THPD	D Average duration of high pulses	8.3	91.0	7.6	8.3	6.5	7.6	22.8	9.1
TLPC	F Low-pulse count (events < T75)	16	1	16	12	14	13	5	10
TLPD	D Average duration of low pulses	5.6	90.0	5.3	7.5	6.4	6.9	18.0	9.0
TMRFR	R Mean rise/fall rate (daily temperature change)	0.79	0.10	0.74	0.49	0.75	0.77	0.33	0.66

Note: Values for Ladybower (columns 4–5), Winscar (columns 6–7) and version 1 of the Derwent non-regulated site ('C_v1'; column 8) were calculated for the period June 1, 2017–May 31, 2018; values for version 2 of the Derwent non-regulated site ('C_v2'; column 9) and regulated sites (columns 10–11) were calculated for the period February 1, 2017–January 31, 2018. Thermal regime components: M = Magnitude; T = Timing; F = Frequency; D = Duration; R = Rate-of-change.

Reservoir and Ladybower Reservoir and for the sample site upstream of Derwent Reservoir, all available water temperature measurements were used to fit the GAMs. The fitted models were subsequently used to predict daily water temperatures for the period 2012–2016 for each site. For both regulated sites downstream of Derwent Reservoir, GAMs were fitted for the period February 1, 2017–February 28, 2018, coinciding with a period of near-continuous operation of the Kielder Water transfer (see also Figure 4). Substantial differences in downstream water temperature patterns were observed between periods with and without the water transfer in operation (see Section 3.1 below for further description). During the period 2012–2016, the water transfer was only in operation during May–November 2015 (6 months) and September–November 2016 (2 months). As insufficient water temperature measurements for periods without water transfer were available between November 2016 and February 2019 to fit a separate GAM, extrapolated water temperature series were corrected for days in 2012–2016 when the water transfer was not in use (Section 2.1). A monthly correction factor was derived from differences in the upstream–downstream monthly temperature difference between months with and without water transfer (Table 2). During months in which this comparison was not possible, correction factors were estimated based on neighbouring months. All models were highly significant ($p < 0.001$; RMSE = 0.41–0.82) and accounted for >95% of the variation (explained deviance) between air temperature and water temperature.

We examined in-stream community responses to various indices reflecting different thermal magnitudes (i.e., minimum, mean and

maximum). This approach was undertaken as the vast majority of research demonstrating the ecological importance of thermal regimes (e.g., direct impacts on the metabolic rates and physiology of freshwater biota) have explored stream temperature magnitudes (Olden & Naiman, 2010). Antecedent temperature magnitudes occurring across varying durations were considered so that short- and long-term ecological responses could be considered, including the intra- and inter-seasonal effects of stream temperatures on instream biota. Mean, minimum and maximum daily water temperatures were derived from the modelled water temperature time series for three antecedent periods for every ecological sample: (a) 30 days (short-term); (b) 90 days (mid-term); and (c) 365 days (long-term), yielding nine temperature indices. The effect of each thermal index on individual response variables was examined using linear regression modelling techniques. Separate tests were constructed for values corresponding to each season (to separate the effects of intra-annual life-cycle and temperature variations) and site position (i.e., non-regulated versus regulated—allowing the effect of flow regulation on temperature–ecology relationships to be explored). The significance of each linear model was tested via a one-way Analysis Of Variance (ANOVA). The results of linear regression analysis between the individual thermal indices and ecological response variables were summarised in heat maps, presenting the explained variance (R^2), as well as individual scatter plots between thermal indices and response variables. Season and site type are indicated in the scatter plots using different colours and symbols.

TABLE 2 Monthly mean water temperature differences at Derwent Reservoir

Month	Regulated 1		Regulated 2		Tyne
	T	NT	T	NT	
January	0.7	0.3	0.3	0.0	0.8
February	0.6	0.3	0.2	0.3	1.0
March	0.9	0.2	0.7	0.6	1.0
April	1.1	−0.8	1.0	0.6	1.8
May	1.7	−2.2	1.3	0.1	3.3
June	2.8	N/A	1.7	−0.6	3.0
July	2.4	−3.1	1.6	−0.8	2.1
August	2.4	−1.0	1.4	0.0	2.2
September	2.1	N/A	1.2	N/A	1.8
October	1.8	N/A	1.1	N/A	1.3
November	1.4	1.7	0.6	0.7	1.1
December	0.6	0.3	0.0	0.0	0.7

Note: Column 2–5: temperature differences (°C) between regulated and non-regulated sample sites (downstream–upstream) at Derwent Reservoir during months with (T) and without Kielder transfer compensation flow in operation (NT); column 6: differences (°C) between River Tyne and unregulated River Derwent. N/A indicates months for which no water temperature data without the influence of the Kielder transfer was available. Italicised values are based on incomplete months or involve months with water transfer for part of the month.

3 | RESULTS

3.1 | Thermal alteration downstream of reservoirs

Thermal regimes for the period June 2017–May 2018 at non-regulated (upstream) sites were very similar across the three reservoirs (Table 1, columns 4, 6 and 8). Maximum daily temperatures (*TMAX*) ranged from < 16°C upstream of Winscar Reservoir to > 17°C upstream of Ladybower Reservoir, occurring between mid-June and mid-July 2017. Minimum temperatures (*TMIN*) were around 0°C upstream for all reservoirs and occurred at the end of February 2018. Water temperature patterns at the non-regulated sites were congruent with air temperature, although water temperature peaks and troughs were typically less extreme, with differences up to 4°C (Figures 2–4).

The greatest differences between upstream and downstream thermal regimes were recorded at Ladybower Reservoir (Figure 2). Downstream water temperatures were generally lower than upstream during spring and summer (April–August), with up to 5°C reductions in May. During autumn and early winter (September–December), temperatures downstream were on average higher than upstream, up to 3°C higher in November. A substantial lagged response was observed for the timing of the annual maximum temperature (almost 100 days) and to a lesser extent the annual minimum temperature (c 17 days). Rise/fall rates were strongly reduced from 0.79 to 0.1 degrees/day. In

FIGURE 2 Daily water temperature upstream and downstream of Ladybower Reservoir, as well as daily air temperature (May 2017–June 2018). Black = upstream; red = downstream; grey = air temperature (station 525, Sheffield) [Color figure can be viewed at wileyonlinelibrary.com]

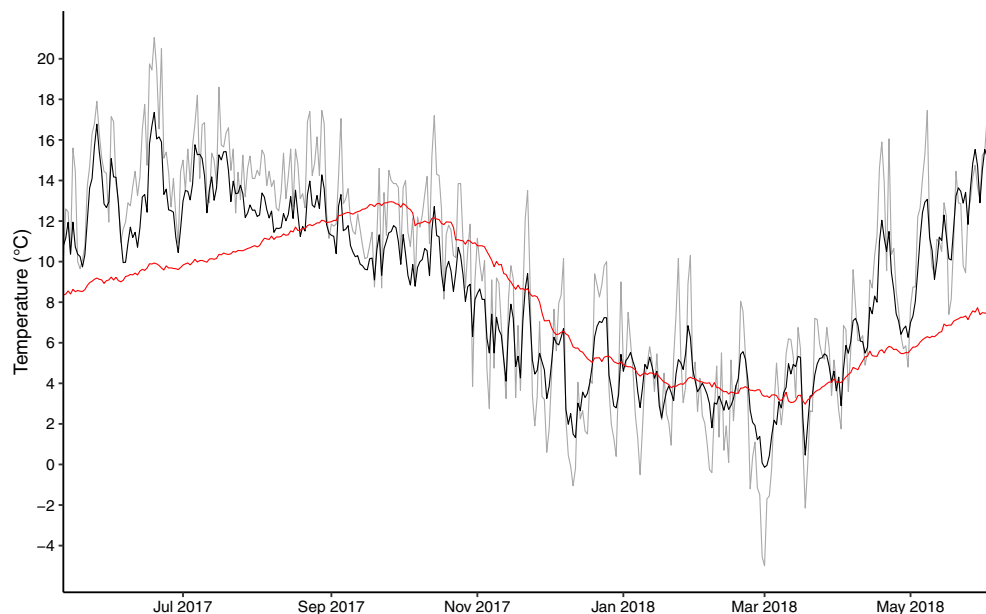
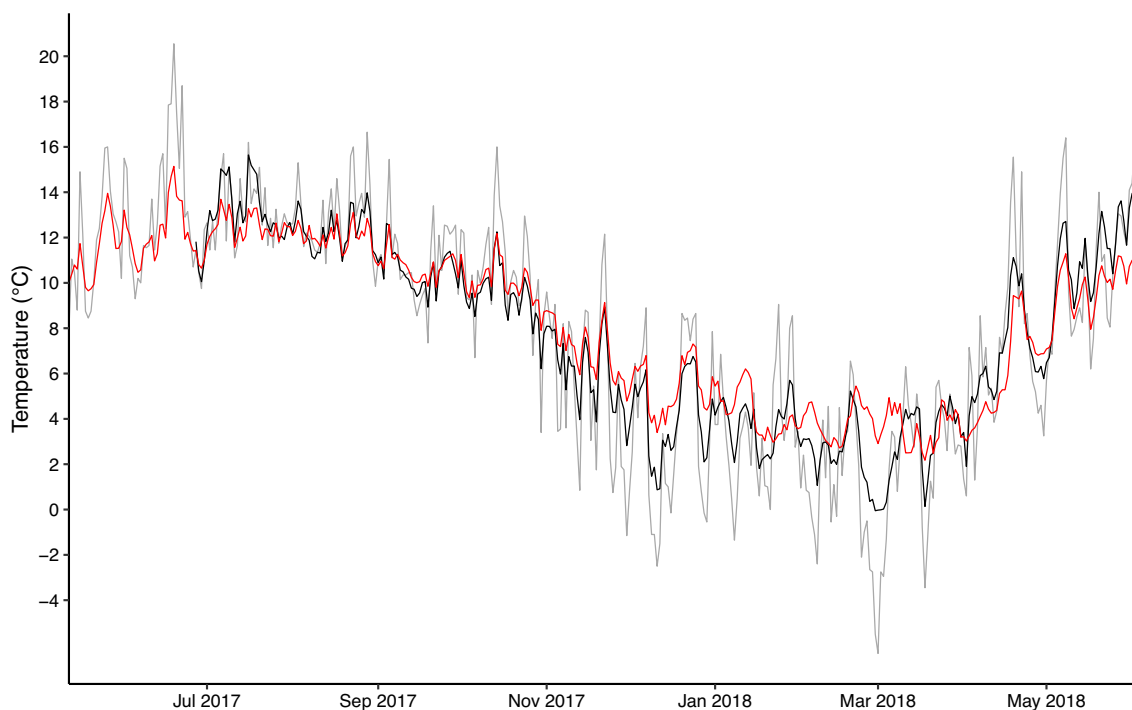


FIGURE 3 Daily water temperature upstream and downstream of Winscar Reservoir, as well as daily air temperature (May 2017–June 2018). Black = upstream; red = downstream; grey = air temperature (station 56958, Emley Moor nr2) [Color figure can be viewed at wileyonlinelibrary.com]

contrast to the non-regulated sites, no clear high and low pulses were recorded at the Ladybower regulated site.

The water temperature regime downstream of Winscar Reservoir (Figure 3) was similar to the paired non-regulated site, with modest differences for thermal extremes. Maximum temperatures appeared lower (up to 1°C in May) and minimum temperature were higher (up to 1.5°C in December and February). Some changes in the timing of annual maximum (up to 29 days earlier) and minimum temperatures

(up to 17 days later) were recorded, but the timing of annual maximum temperature may have been influenced by missing summer temperature data at the start of the time series. Rise/fall rates were slightly reduced compared to upstream, from 0.74 to around 0.49°/day.

At Derwent Reservoir, water temperatures downstream were higher than upstream throughout the period 1st February 2017–31st January 2018, both for monthly mean and annual minimum and

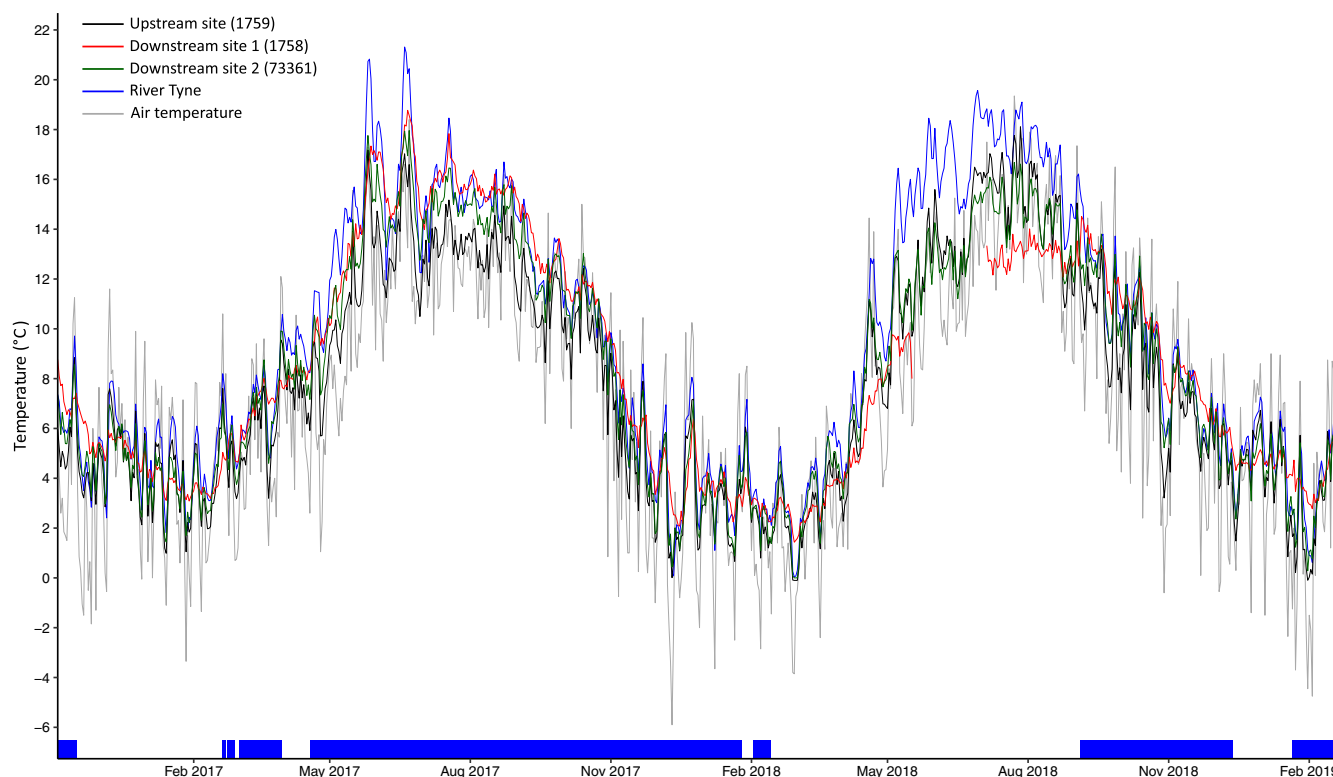


FIGURE 4 Daily water temperature upstream and downstream of Derwent Reservoir, as well as daily air temperature and River Tyne water temperature (November 2016–February 2019). The bottom blue bar indicates the period of Kielder water transfer operation [Color figure can be viewed at wileyonlinelibrary.com]

maximum temperatures (Figure 4). The pattern was clearest at the first regulated site (closest to the reservoir), with an average increase of nearly 3°C in June, but was also recorded further downstream, with the difference being greatest for summer temperatures (c 1.5°C). Regulated sites experienced fewer high and low pulses with on average a longer duration, although the difference was limited at the second regulated site. Rise/fall rates were reduced at the first regulated site (from 0.77 to around 0.33 degrees/day), while reductions at the second regulated site were limited (to around 0.66 degrees/day).

The differences in monthly mean water temperatures between regulated and non-regulated sites at Derwent are presented in Table 2 for both periods with and without Kielder Water transfer compensation flows (columns 2–5). During the water transfer operation, monthly mean water temperatures at the first regulated site were higher in every month. Increases were greatest during the summer (nearly 3°C in June) and lowest during the winter (0.6–0.7°C higher in December–February). During the period without water transfer, monthly downstream temperatures were lower than upstream temperatures between April and August (≥ 5 months), with reductions of more than 3°C in July. From this, it follows that the mean downstream July temperature during water transfer was more than 5°C higher than without water transfer. During the winter period, downstream temperatures were on average higher than upstream temperatures, but differences were typically less than in the period subject to water transfer. A similar pattern was observed

for the second regulated site, although absolute differences were typically less. During the period without water transfer, regulated–non-regulated differences were less than 1°C. Monthly water temperatures in the River Tyne were generally more than 1°C higher than in the River Derwent (non-regulated sample site), with the greatest differences ($> 3^\circ\text{C}$) in May–June (Table 2, column 6).

3.2 | Association between water temperature and community response variables

For all response variables, temperature–ecology association patterns differed substantially between site types (i.e., regulated versus non-regulated) as well as seasons (see heatmap in Figure 5). At regulated sites, the macroinvertebrate index WHPT (Figure 6; Tables S1 and S2) broadly displayed positive associations with the most extreme thermal index values, with the highest WHPT values recorded for the highest maximum and lowest minimum temperature. For spring samples, WHPT values were significantly lower for higher values of Min90 ($R^2 = 0.41$, $p = 0.006$). For autumn samples, WHPT values were significantly higher for greater values of Max30 and Max90 ($R^2 = 0.28$ – 0.43 , $p = 0.003$ – 0.019). For the 1-year antecedent period, associations with Min365 (negative) and Max365 (positive) were significant for both spring and autumn samples ($R^2 = 0.22$ – 0.61 , $p = 0.001$ – 0.043). Patterns at non-regulated sites were markedly

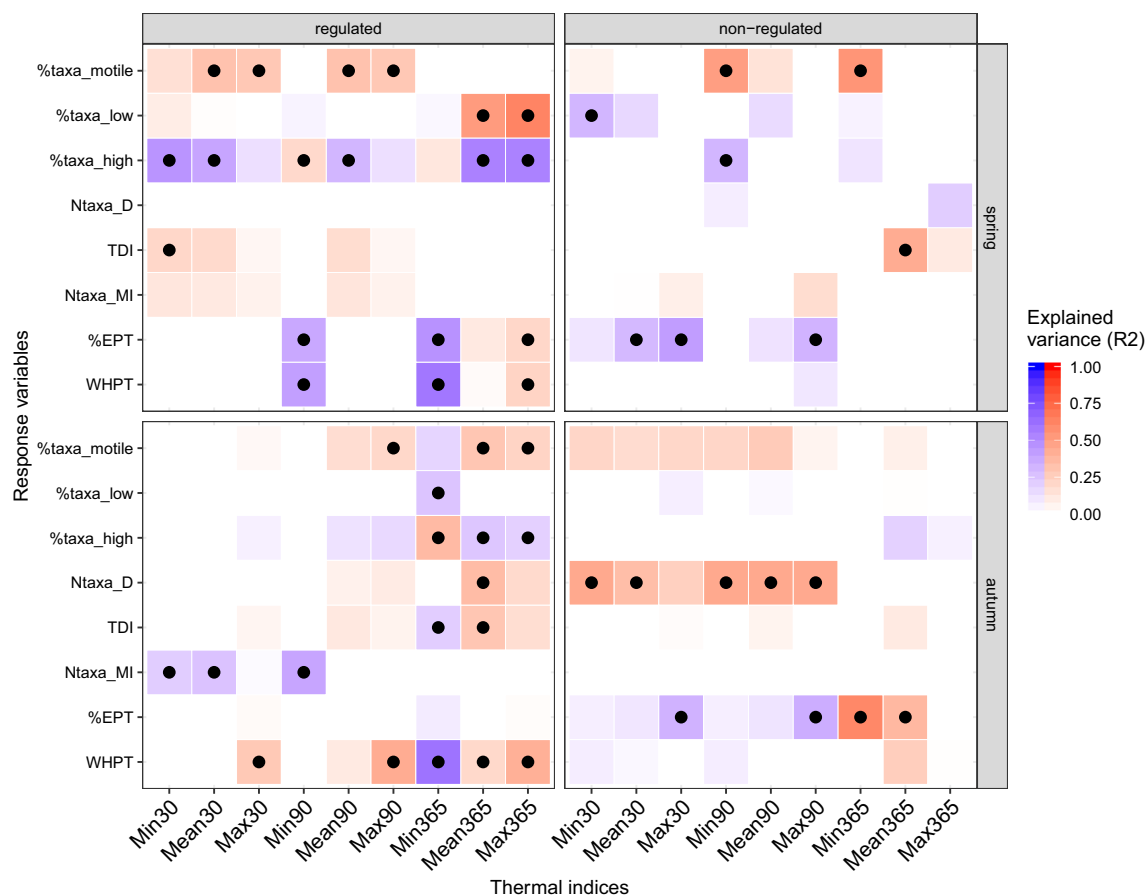


FIGURE 5 Heat map presenting the variance explained (R^2) by linear regression models between individual thermal indices and response variables for spring (top) and autumn samples (bottom), at regulated (left) and non-regulated sites (right). Thermal indices represent minimum, mean and maximum temperature (Min/Mean/Max) for 30-, 90- and 365-day antecedent periods. Response variables include both macroinvertebrate (WHPT, *Ntaxa_MI*, %EPT) and diatom indices (TDI, *Ntaxa_D*, %taxa_high, %taxa_low, %taxa_motile). Significant associations are indicated with a black dot. Red colours represent positive associations and blue colours represent negative associations [Color figure can be viewed at wileyonlinelibrary.com]

different: WHPT values were higher than at regulated sites (Figure 6), but no clear associations with thermal indices were observed.

At regulated sites, %EPT values (Figure 5 and Figure S1; Tables S1 and S2) were significantly lower for higher values of Min90 and Min365 for spring samples ($R^2 = 0.37\text{--}0.47$, $p = 0.003\text{--}0.009$), similar to results for WHPT. %EPT values derived from autumn samples displayed no differences with any temperature indices, in contrast to WHPT. At non-regulated sites, values for %EPT were generally higher than at regulated sites (Figure S1). Significantly lower %EPT values were observed for higher values of short-term indices Max30 and Max90 for both spring and autumn samples ($R^2 = 0.32\text{--}0.42$, $p = 0.013\text{--}0.031$), contrasting with the results for regulated sites. For autumn samples, positive associations were also observed for Min365 and Mean365 ($R^2 = 0.37\text{--}0.60$, $p = 0.002\text{--}0.021$).

For *Ntaxa_MI*, associations with temperature indices at regulated sites were weaker than for WHPT or %EPT (Table S1) with a large spread in the scatter plots (Figure S2). For shorter antecedent periods, significant negative associations were observed for Mean30, Min30 and Min90 during autumn ($R^2 = 0.21\text{--}0.38$, $p = 0.006\text{--}0.04$), whereas

the associations with these indices appeared positive (but were not significant) for spring samples. No significant associations were observed between *Ntaxa_MI* and thermal indices characterising longer antecedent periods (Min365, Mean365 and Max365). Values for *Ntaxa_MI* were lower at non-regulated sites (Figure S2 and Table S2), but no clear associations with thermal indices were recorded.

Associations between thermal indices and the diatom index TDI (Figure 7; Tables S3 and S4) at regulated sites were generally positive, especially for autumn samples. Significantly higher TDI values were observed for higher values of Mean365 ($R^2 = 0.30$, $p = 0.017$), although a significant negative association was found for Min365 ($R^2 = 0.21$, $p = 0.042$). At non-regulated sites, no clear patterns were observed, except for some positive associations with Mean365 (significant for spring samples, $R^2 = 0.43$, $p = 0.017$).

For *Ntaxa_D* (Figure S3; Tables S3 and S4), no significant associations were observed for spring samples from regulated sites. For autumn samples, associations were typically positive for the 1-year antecedent period, testing significantly for Mean365 ($R^2 = 0.35$, $p = 0.009$). At non-regulated sites, no patterns were observed for

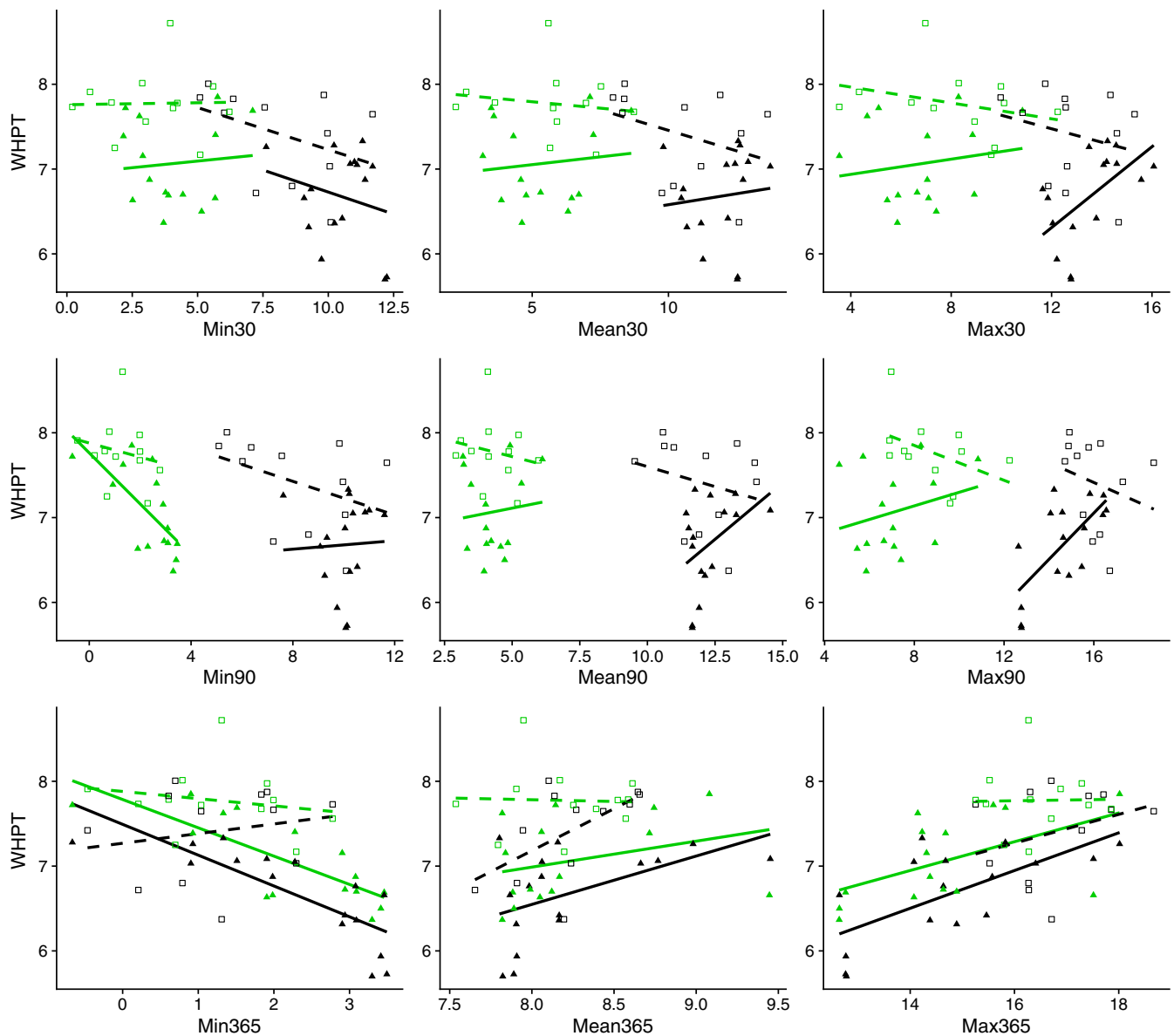


FIGURE 6 Associations between thermal indices and Walley-Hawkes-Paisley-Trigg index (WHPT) scores. Thermal indices represent minimum, mean and maximum temperature (Min/Mean/Max) for 30-, 90- and 365-day antecedent periods. Green = spring, black = autumn; closed triangles and solid line = regulated sites, open squares and dashed line = non-regulated sites [Color figure can be viewed at wileyonlinelibrary.com]

spring samples, but positive significant associations with thermal indices based on 30-day and 90-day antecedent periods were observed for autumn samples ($R^2 = 0.34\text{--}0.45$, $p = 0.015\text{--}0.035$). Values for both TDI and *Ntaxa_D* were typically higher at regulated sites than at non-regulated sites (Figure 7 and Figure S3).

Considering the diatom ecological guilds, %*taxa_motile* showed similar patterns to TDI at regulated sites, especially for autumn samples, with generally positive associations with thermal indices (Figure S6; Tables S3 and S4). For spring samples, %*taxa_motile* values were significantly higher for greater indices values associated with short-medium-term periods (30- and 90-day; $R^2 = 0.29\text{--}0.32$, $p = 0.013\text{--}0.019$), but not for the 1-year antecedent period. For autumn samples, significant associations were observed for Mean365

and Max365 ($R^2 = 0.23\text{--}0.30$, $p = 0.017\text{--}0.036$). At non-regulated sites, significant positive associations were observed for Min90 and Min365 during spring ($R^2 = 0.50\text{--}0.54$, $p = 0.006\text{--}0.009$), but not for autumn samples. Values for %*taxa_motile* were typically higher at regulated sites than at non-regulated sites.

For %*taxa_high* (Figure S4; Tables S3 and S4) at regulated sites, associations were largely negative. For spring samples, lower %*taxa_high* values were significantly associated with higher temperature index values reflecting short antecedent periods (especially 30-day; $R^2 = 0.39\text{--}0.46$, $p = 0.002\text{--}0.006$) as well as the 1-year antecedent period (Mean365 and Max365; $R^2 = 0.54$, $p < 0.001$). For autumn samples, associations were generally stronger for the 1-year period ($R^2 = 0.20\text{--}0.36$, $p = 0.009\text{--}0.048$) and appeared opposite to those

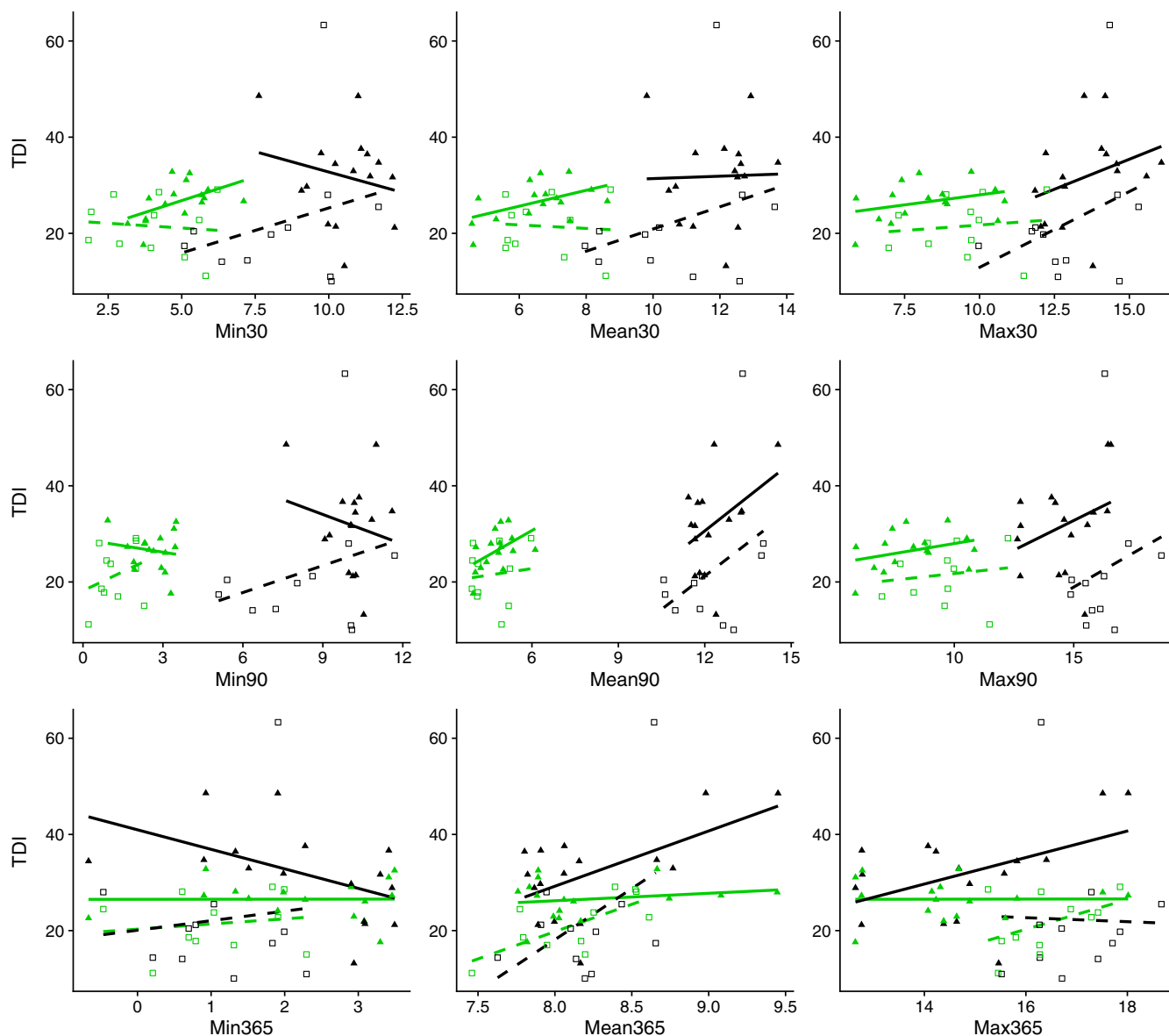


FIGURE 7 Associations between thermal indices and Trophic Diatom Index (TDI) scores. Thermal indices represent minimum, mean and maximum temperature (Min/Mean/Max) for 30-, 90- and 365-day antecedent periods. Green = spring, black = autumn; closed triangles and solid line = regulated sites, open squares and dashed line = non-regulated sites [Color figure can be viewed at wileyonlinelibrary.com]

observed for %*taxa_motile*. No clear patterns were observed at non-regulated sites, although %*taxa_high* values appeared higher than at regulated sites. In general, no clear associations were observed between temperature indices and %*taxa_low* (Figure S5; Tables S1 and S2). For spring samples, significant positive associations were observed for Mean365 and Max365 ($R^2 = 0.51\text{--}0.62$, $p < 0.001$) at regulated sites (opposite to %*taxa_high*).

It should be noted that a 'clustering' of values within individual regulated sites was observed for thermal indices characterising long-term temperature variations (i.e., Min365, Mean365 and Max365), although this trend was not as evident for non-regulated sites. This clustering was less pronounced for thermal indices capturing short-term (Min30, Mean30 and Max30) and intermediate time frames (i.e., Min90, Mean90 and Max90). This clustering was observed for

most biomonitoring metrics, with an example for WHPT added in the Supplementary material (see Figure S7).

4 | DISCUSSION

4.1 | Thermal alteration downstream of reservoirs

The results in the current study demonstrated a marked inter-annual variation of water temperatures at regulated river sites as a result of water management practices, including impoundment and inter-basin transfers. The comparison between the thermal regime at non-regulated and regulated sites demonstrated that the water supply reservoirs substantially modified the downstream thermal regime. The

effect was most obvious downstream of Ladybower reservoir, with distinctly lower summer temperatures (5°C) and higher winter temperatures (3°C), generally leading to a more stable and 'compressed' thermal regime (reduced temperature range). This pattern is comparable to several research outputs examining thermal alteration following impoundment (e.g., Crisp, 1977; Vinson, 2001; Wright, Anderson, & Voichick, 2009). The absolute thermal effects appeared strongest in summer, consistent with previous studies examining water supply reservoirs (e.g., Andrews & Pizzi, 2000; Cowx et al., 1987; Lavis & Smith, 1972; Malatre & Gosse, 1995), although the opposite has also been reported for one UK reservoir (Webb & Walling, 1993). The delay of maximum and minimum temperature has also been reported in other studies in the United Kingdom (Webb & Walling, 1993), United States (Vinson, 2001) and Australia (Preece & Jones, 2002).

Although a general reduction of daily and seasonal temperature fluctuation was observed downstream of all three reservoirs, the exact thermal regime alteration differed across the sites. For example, the effects downstream of Winscar Reservoir were more modest (maximum difference 1–1.5°C) than for Ladybower Reservoir (maximum difference 5°C). Other studies have found that while reservoirs can yield comparable effects (i.e., seasonal increases or decreases) at the regional scale, the magnitude of such changes can differ markedly across individual sites (Lessard & Hayes, 2003; Maheu et al., 2016; Meißner, Schütt, Sures, & Feld, 2018). These observations and the results of the current study emphasise the importance of reservoir characteristics. The temperature measurements at two sites downstream of Derwent reservoir demonstrated that the effects of impoundment on the thermal regime are strongest closer to the reservoir (1 km downstream), but were still apparent at the second regulated site (>6 km downstream). Several studies have indicated that thermal alteration effects can persist considerable distances downstream, depending on site-specific factors including reservoir type, size and operation, and downstream river network characteristics including inflowing tributaries (e.g., Casado et al., 2013; Ellis & Jones, 2013, 2016; Lessard & Hayes, 2003; Malatre & Gosse, 1995). Nonetheless, Webb and Walling (1993) expected the thermal effects of UK reservoirs to be of a local nature and to diminish quickly downstream (<10 km).

Temperatures downstream of Derwent Reservoir were markedly higher than upstream for most of the year during the comparison period, especially during summer and close to the reservoir. The higher temperatures were caused by the operation of the Kielder Water transfer scheme, providing compensation flow downstream of the reservoir using transferred water from the River Tyne, where water temperatures were generally higher than in the unregulated River Derwent. In contrast, when the water transfer was not in operation, the presence of Derwent Reservoir resulted in reduced water temperature in summer. Elevated summer water temperatures have been linked to smaller surface-release reservoirs or reservoirs in cold climatic regions (e.g., Lessard & Hayes, 2003; Malatre & Gosse, 1995; Olden & Naiman, 2010). Large-scale or inter-basin water transfers are a common water management practice around the world including the UK (e.g., Bickerton, 1995; Davies, Thoms, & Meador, 1992;

Soulsby et al., 1999; Zhuang, 2016), but their effects on abiotic and biotic factors remain poorly understood (e.g., Snaddon, Wishart, & Davies, 1998; Zhuang, 2016). Several studies have focused on the hydrological or physico-chemical implications of interbasin-transfer schemes, or how such practices facilitate biological invasions (e.g., Gibbins, Soulsby, Jeffries, & Acornley, 2001; Kroll et al., 2013; Meador, 1992; Prat & Ibañez, 1995). However, there appear to be very few sources in the wider literature studying the effect of water basin transfer schemes on water temperature (but see review by Meador, 1992), although some authors have hypothesised an effect on the thermal regime (Davies et al., 1992; Snaddon et al., 1998). The results of the current study showed that this effect can be substantial.

4.2 | Association between water temperature and macroinvertebrate indices

The analysis of combined thermal indices and macroinvertebrate response variables revealed inconsistent associations across both site types (i.e., regulated versus non-regulated) and seasons. These findings likely reflect either differences in water temperature variations or community compositions between site types and seasons (or a combination of the two). When focusing on regulated site samples only, WHPT and to a lesser extent %EPT values appeared highest at the extreme end of the temperature spectrum, that is, the highest maximum and lowest minimum temperatures. Combined with the recorded thermal effects of water supply reservoirs (reduced temperatures in summer, increased temperatures in winter), these associations highlighted the negative implications of cold- and warm-water 'pollution' (sensu Olden & Naiman, 2010) in summer and winter, respectively, for macroinvertebrate communities. The seasonal difference in responses was anticipated, as the dampening effect of reservoirs on maximum temperatures was likely to be strongest during summer, when air temperatures are higher. Equally, the increase of minimum temperatures was expected to be strongest during winter. In addition, responses of WHPT appeared strongest to thermal indices based on longer antecedent time periods, indicating the effect of long-term thermal changes rather than short-term variability on this bio-monitoring index. This could be in part due to the nature of the reservoirs studied, whereby thermal alterations are less abrupt in the short-term relative to other types of the reservoir (e.g., hydropower). Long-term thermal metrics encompassing alterations spanning multiple seasons are more likely to affect a larger number of taxa and their life-cycle strategies, including warmer winter temperatures altering larval development (Durance & Ormerod, 2007) or colder summer temperatures changing adult emergence strategies of aquatic insects (Lehmkuhl, 1972).

Other studies on EPT taxa considered cold-water stress in summer the most important pressure (Phillips et al., 2015; Stevens et al., 1997). Lessard and Hayes (2003) found a substantial reduction of EPT taxa linked to increased summer temperatures, which may be analogous to downstream of Derwent Reservoir during the operation of the Kielder Water transfer (autumn 2015 and autumn 2016).

However, this could not be tested in the current study, since the extrapolated water temperature series only contained reduced summer temperatures. We found that the total richness of macroinvertebrate communities typically showed a limited response to changes to minimum, average or maximum temperatures downstream of the reservoirs. Several studies in the literature have related observed reductions in taxa richness to temperature changes (e.g., Benítez-Mora & Camargo, 2014; Jackson et al., 2007), although Lessard and Hayes (2003) did not observe changes to taxa richness downstream of surface-release reservoirs associated with increases in summer temperature.

The WHPT index was developed as an update of the BMWP methodology, originally derived to assess the biological water quality/health of rivers in the United Kingdom by considering taxa tolerances to nutrient enrichment (Paisley et al., 2014). Although water temperature did not feature explicitly in the development of the index, it is routinely considered a fundamental component of water quality, specifically due to the intrinsic negative relationship between dissolved oxygen and water temperature under comparable natural conditions. The fact that WHPT scores in the current study were typically lower at regulated (downstream) than at non-regulated (upstream) sites, may point to a reduced water quality below reservoirs as a result of discharge from the reservoir, potentially through phenomena like nutrient enrichment. As such, the positive association between WHPT and temperature within regulated sites seems counterintuitive given this indicates a greater number of pollution-sensitive taxa occurring when dissolved oxygen levels are lower. However, dissolved oxygen may not have represented a limiting factor for macroinvertebrate communities in the regulated sites studied. Instead, higher summer temperatures in regulated systems (which are still lower overall due to the reservoir) may have produced thermal conditions more akin to the natural settings which meet their thermal requirements, whilst still maintaining sufficient dissolved oxygen levels, potentially due to the presence of riffle habitats immediately downstream of the dam. It should be noted that in a recent UK study, Aspin, House, Martin, and White (2020) found that WHPT responses to thermal indices were obscured by the trophic status of the reservoir and indicated the interactive effects of nutrient and thermal regimes on this bio-monitoring index, which may also help to explain some of the results reported in the present study. Further research is required to integrate further abiotic environmental controls, including river discharge, substrate characteristics and nutrient regimes, to be analysed interactively with water temperature data. In addition, a clustering of thermal index values characterising longer-term temperature regimes (i.e., 365-days prior to sample collection) was observed from individual regulated sites (see Figure S7), likely reflecting the uniqueness of thermal regimes (and magnitudes specifically) being captured more readily compared to shorter temporal scales. While this may have potentially affected thermal-ecology statistical associations, the high amount of explained variance within some of these models (e.g., WHPT versus Min365 and Max365) highlights the ecological importance of such long-term thermal magnitude metrics. Nevertheless, further research could be required to account for the potential effects of pseudo-replication

when constructing thermal-ecology relationships in regulated systems, particularly alongside other environmental controls.

For most biomonitoring indices, thermal-ecology relationships observed for non-regulated (upstream) sites were markedly different from regulated (downstream) sites. This is an indication of the contrasting biotic communities upstream and downstream of reservoirs created by a multitude of environmental controls (e.g., nutrient regimes, flow and habitat). Lastly, weaker ecological responses to thermal indices in non-regulated environments are likely indicative of the more dynamic nature of these headwater sites, where local conditions, including water temperature, are even more variable (White et al., 2017). Functional trait assessments may have afforded a causal understanding the ecological responses to thermal controls in regulated versus non-regulated environments, such as through changes in maximum body size or voltinism (White et al., 2017). However, the family-level data used in this study may overlook species-specific trait information that may obscure a reliable understanding of thermal-ecology relationships (Hamilton et al., 2020). Further research is required to better understand findings like those presented here on functional responses to thermal alterations within regulated and non-regulated environments.

4.3 | Association between water temperature and diatom indices

The analysis of combined thermal indices and diatom response variables yielded inconsistent associations across both site types and seasons, similar to the results for macroinvertebrates. At regulated sites, diatom community responses to thermal controls in autumn appeared to differ from spring. Autumn communities were typically sensitive to 1-year antecedent temperatures. This seems counter-intuitive since diatom communities typically respond more quickly to environmental changes relative to larger-bodied organisms (e.g., macroinvertebrates) due to their more rapid generation times, although a causal understanding is not clear. In contrast, spring communities also appeared sensitive to short-term antecedent temperatures (30-day and 90-day) which reflected the temperatures of the preceding winter. During autumn, diatom indices including TDI and %*taxa_motile* appeared highest at the extreme end of the temperature spectrum, that is, the highest maximum and lowest minimum temperatures (similar to the macroinvertebrate index WHPT), indicating negative effects of cold-water 'pollution' in summer. This effect was largely absent for diatom communities in spring, indicating a seasonality in diatom community response to thermal controls. Associations between thermal controls and %*taxa_high* appeared the opposite of some of the associations observed between thermal controls and TDI, %*taxa_low* and %*taxa_motile*, that is, lower values for higher mean and maximum temperatures. Literature on benthic diatoms in association with thermal changes in impounded rivers is rare (but see Elias, Vieira, Feio, & Almeida, 2012). Blinn et al. (1989) incubated benthic diatoms, which were collected downstream of Glen Canyon Dam, United States, under different temperatures in a laboratory setting and found that a

number of high-profile taxa were strongly reduced at higher temperatures, whereas some low-profile taxa increased. These findings are in keeping with our results for high-profile taxa (generally decreased for higher temperatures) and for associations of spring community low-profile taxa with 1-year antecedent temperatures (increased for higher temperatures). It should be noted that Blinn et al. (1989) observed the changes after 2 weeks of incubation, whereas in the current study the associations with the thermal regime were observed for both short-term and long-term temperature indices. The sensitivity of diatom communities to longer-term antecedent temperatures could not be explained in this study. It is possible that besides short-term changes, diatom communities also respond to environmental changes that occur at a longer term, but this warrants further study.

At non-regulated (upstream) sites, no significant associations between diatom communities and thermal indices could be observed. As suggested for macroinvertebrate communities, this could be an indication of the contrasting communities upstream and downstream of reservoirs due to multiple environmental controls, combined with the dynamic nature of headwater sites. Nevertheless, combined with the findings for regulated sites, it is hypothesised that other environmental controls, for instance water quality, are potentially more important drivers of diatom community changes than thermal controls (see Bergey, Desianti, & Cooper, 2017). Future research should consider a wider range of environmental controls, including river discharge, substrate composition and nutrient loads, to allow the exploration of the combined effects of multiple abiotic factors at both regulated and non-regulated sites, whilst accounting for the potential effects of pseudo-replication that was not explored in this study.

4.4 | Study implications

Our study is one of the first to analyse high-resolution, continuous water temperature measurements alongside a range of both macroinvertebrate and diatom response metrics. The temperature measurements clearly showed the effect of river impoundment on riverine thermal regimes. In addition, our findings indicate that site-specific thermal modifications and inter-annual variability are important factors to include in studies of the thermal impact of river impoundment. In the current study, an inter-basin water transfer scheme had a marked effect on the thermal regime, an aspect that has rarely been described in previous research. Despite the fact that high-resolution water temperature data were available for a relatively short period (2 years for Derwent Reservoir), our study clearly illustrated major variation between years as a result of management operations. To obtain greater insights into the effects of water supply reservoirs on thermal patterns, as well as to increase the predictive power of modelled temperature time series, long-term monitoring is vital.

We observed that macroinvertebrate communities and diatom assemblages appeared to respond differently to thermal modifications, in terms of both magnitude and time scale, indicating that these ecological groups provide different information about river regulation for water managers. Temperature monitoring initiatives included within

river management strategies often comprise individual spot-check measurements (or are neglected entirely), which significantly restricts the potential to examine modifications to stream temperatures. The results here highlight the need for long-term, continuous temperature measurements to be collected alongside biomonitoring data across regulated and non-regulated systems encompassing multiple reservoirs to better understand the ecological effects of thermal alterations driven by impoundment. Specifically, our results reiterate the need for long-term, continuous thermal regime data (beyond standard water quality testing) to help guide management strategies in regulated rivers. This need is emphasized by the fact that water temperature in the year prior to sampling yielded similar or greater ecological effects compared to short-term temperature variations. In addition, future studies should seek to include temperature indices based on the other thermal regime components characterising the frequency, duration, timing and rate-of-change, rather than only including the magnitude component. Finally, there is a pressing need to study the ecological importance of thermal regimes (and their different components) alongside other environment controls (e.g., water quality, flow and habitat conditions) in order to more effectively guide sustainable water resource management operations.

5 | CONCLUSIONS

This study presents the analysis and results of near-continuous water temperature measurements to quantify thermal alteration at regulated sites downstream of three water supply reservoirs compared to non-regulated sites and its effects on downstream biotic communities. We demonstrated that water supply reservoirs reduced downstream thermal variability, with reduced summer temperatures and increased winter temperatures. We also observed that the timing of annual minimum and maximum temperatures was delayed. In addition to this, marked differences in thermal regime modifications between reservoirs emerged, as well as a marked inter-annual variation related to management practices (water transfer) downstream of one reservoir. This highlights the effect of site-specific factors in thermal alteration and emphasises the importance of long-term water temperature monitoring at reservoirs. A number of macroinvertebrate (e.g., WHPT and %EPT) and diatom indices (e.g., TDI and %taxa_motile) were associated with higher maximum summer temperatures and lower minimum winter temperatures, suggesting a negative effect of reduced thermal variation downstream of reservoirs. Macroinvertebrate and diatom communities showed some different responses to thermal modifications, indicating that these ecological groups provide different information about river regulation and the associated implications for water temperatures. At the same time, contrasting communities at regulated and non-regulated sites were observed for both ecological groups, an indication of the contrasting biotic communities upstream of downstream of reservoirs due to multiple environmental controls. We recommend including longer-term, continuous water temperature monitoring at both regulated and non-regulated river sites across multiple reservoirs, and conducting thermal experiments to test the

ecological effect of changes to thermal regime components other than magnitude, ideally in combination with other abiotic controls. This will ultimately facilitate the inclusion of the thermal regime into e-flow research and implementation.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, [HJK], upon reasonable request.

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