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The effects of a thermal discharge on the macro-invertebrate community of a large British river: Implications for climate change.

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Abstract

Anthropogenic changes to the temperature regimes of rivers, whether through thermal pollution, removal of shade or climate change, could affect community stability and cause phenological changes in aquatic species. This study examines the impact of a thermal discharge from a power station on the diversity and composition of the aquatic macro-invertebrate community in the River Severn, UK. Daily temperatures up to 2 km downstream of the thermal discharge averaged 4.5°C above ambient. Abundance and taxon richness metrics were reduced at a site approximately 0.5 km downstream of the power station outfall, but were largely unaffected at a second site about 2 km downstream. The majority of the macro-invertebrate taxa observed were recorded at both control and heated sites, suggesting species were below their thermal tolerance threshold or had developed adaptations to survive increased temperatures. However, indicator species analysis suggests certain taxa were associated with particular sites; abundances of *Musculium lacustre*, *Simulium reptans* and Orthocladiinae were greater at the unheated control site, whereas more pollution-tolerant species such *Asellus aquaticus* and *Erpobdella octoculata* were more common in the thermally impacted reaches. Overall, the results provide an indication of potential species and community response to future warming under climate change scenarios.

Keywords: Climate change; macro-invertebrates; community composition; thermal pollution; taxonomic richness.

Introduction

Human activities have severely degraded many of the world's freshwater systems, particularly rivers, over many years (e.g., Hawkes, 1956; Hynes, 1960; Revenga et al., 2000), with recent rapid human population growth increasing the stress on global water resources (Duda & El-Ashry, 2000). The combination of multiple stressors, including pollution, habitat fragmentation and loss, land-use changes, and over-exploitation, has resulted in declines of many indigenous species and relatively high extinction rates for freshwater organisms (Ricciardi & Rasmussen, 1999; Revenga et al., 2000; Jenkins, 2003; Dudgeon et al., 2006). Temperature is considered one of the most important physical influences on both the composition of macro-invertebrate communities and on phenology of individual species (Hynes, 1960; Langford, 1990). Among the many anthropogenic activities which have directly or indirectly caused changes in river temperatures and aquatic biota are tree-clearance, impoundments and thermal discharges from power stations and other industries (Langford, 1983, 1990; Caissie, 2006; Broadmeadow, et al. 2011).

Since the late 19th century, global average air temperatures have increased by almost 0.8°C (Jenkins et al., 2008) and are projected to rise further (Bates et al., 2008; IPCC, 2013). Temperatures of some UK rivers indicate warming over the last 20 to 30 years (Hammond & Pryce, 2007), although the closure of direct-cooled power stations has resulted in cooling of certain reaches (Langford et al., 2012). Summer temperatures in some UK river systems are predicted to rise by up to 4°C (Johnson et al., 2009), while changes in precipitation and evapotranspiration are expected to increase the frequency of drought and flood episodes (Hulme et al., 2002; Wilby et al., 2010; Watts et al., 2013). Due to the relationship between climate patterns and fluvial processes and the interaction with other stressors, freshwater environments are considered to be some of the systems most sensitive to climate change (Durance & Ormerod, 2009).

Whilst some broad predictions of river warming impacts can be made on the basis of prior research or forecasting modelled species distribution (e.g., Durance & Ormerod, 2007; Domisch et al., 2013), their accuracy necessarily remains unknown until such time that more highly elevated temperatures occur (Hulme et al., 2002). Further, determining the response of river macro-invertebrates to climate change is impeded due to the absence of information on ecological preferences for the majority of species (Heino et al., 2009). In this regard, historical records of rivers impacted by thermal pollution may be highly instructive (Woodward et al., 2010). Studies over the past 50 years have shown a range of responses to disturbance from thermal discharges at community and species levels in temperate rivers (e.g., Langford, 1971, 1983, 1990). Power station thermal discharges have affected a range of aquatic organisms including fish, algae, bacteria and macrophytes (Langford, 1983, 1990), and inform our understanding of both organism and ecosystem resilience to thermal stress.

At the community level, thermal discharges from power station outfalls have been associated with changes in composition such as a reduction in the abundance of temperature-sensitive species (Obrdlík et al., 1979), an increase in the abundance of temperature-tolerant taxa (Aston, 1973), reduced standing crop (Durrett & Pearson, 1975), and the creation of conditions suitable for non-native species (Howells, 1983). In addition to a higher risk of mortality for temperature-sensitive taxa (e.g., Dallas & Ketley, 2011), temperature increases are also thought to affect species phenology in the form of reduced life cycle length and earlier hatching and emergence (Langford, 1971; Langford & Daffern, 1975; Aston & Milner, 1980).

Historic data from observations during periods of marked thermal pollution from power generation offer direct evidence of the impacts on macro-invertebrates of river temperature increases similar to those predicted by climate models (Hulme et al., 2002). The aim of this study was therefore to assess the effects of a thermal outfall from a direct-cooled power station on the diversity and composition of the benthic macro-invertebrate fauna of the River Severn, UK.

Materials and methods

Site characteristics and sampling

The study was carried out in the vicinity of the Ironbridge ‘A’ power station on the upper-middle reaches of the River Severn, UK (Fig. 1). This reach was selected because of the lack of upstream industrial pollution, high macro-invertebrate diversity and the presence of many pollution-sensitive taxa (Langford & Daffern, 1975). Also, the power station used a large proportion of the river flow during periods of low discharge resulting in high downstream temperatures, while there was little trace of chlorine or other anti-foulants which can complicate thermal discharge effects in more polluted rivers (Langford, 1970, 1971). The River Severn is the longest river in the UK, rising in the Cambrian Mountains, Wales (headwaters 741m above Ordnance Datum), flowing east then south for 354km until it reaches the Bristol Channel (Jones et al., 2012). In the Ironbridge area the River Severn alternates between slow deep reaches and short riffles as it passes through the Ironbridge Gorge (Langford, 1970, 1971). Water chemistry measurements upstream and downstream recorded dissolved oxygen (mgl^{-1}) 9.2–14.8, ammonia (NH_3 mgl^{-1}) 0–0.94 and pH 7.6–8.4, and were similar between the two sites (Langford, 1971). Ironbridge 'A' power station was commissioned in 1932 and had a maximum potential output of 210 MW. The station consisted of four direct-cooled generating units, with 15.2 m^3s^{-1} of river water being passed through the cooling system at peak output. During the study period, Ironbridge 'A' was operating for approximately 15–17 hours per day and water usage could exceed more than 50% of the river flow in low discharge periods. Depending on the extent of power generation and the river discharge, the thermal discharge resulted in increases of up to 8^{o}C at the downstream sampling sites used in this analysis, with elevated temperatures (+5^{o}C) recorded up to 5 km downstream of the power station (Langford, 1970). Maximum temperatures during the period 1965-75 were 22^{o}C at the upstream sampling site and 29.5^{o}C at the downstream site. The maximum effluent temperature in the same period was 31.5^{o}C measured 50 m downstream of the outfalls (Langford, *unpublished data*). Diurnal variation contrasted between the sites with upstream daily temperature fluctuations confined to periods of very high air temperatures or very low flows. Downstream of the power station, temperature peaks occurred during the middle of the day, in response to power station activity (Langford, 1970). There was no measurable thermal stratification at the downstream site, indicating that the river water had been completely mixed with the power station effluent 2 km downstream of the outfall (Langford, 1970).

Over the period of June 1965 to May 1984 a total of 232 separate macro-invertebrate samples were taken from in-stream and marginal habitats. Invertebrate sampling was carried out at three survey sites: Abbey Bridge (AB; 500 m upstream of the Ironbridge 'A' outfall), Garage Bend (GB; 600 m below the outfall) and Gasholder (GH; 2 km below the outfall). The physical characteristics of the river at the three survey sites were broadly similar, being fast-flowing riffles (Langford, 1971; Langford & Daffern, 1975), though the Garage Bend site was slightly deeper than the other two sites. Substrate composition at the three sites generally comprised coarse sand overlain with limestone cobbles (3–25 cm); in addition there was some brick and tile debris from demolished furnaces at the Gasholder site (Langford, 1971). A small, historically polluted stream, the Coalbrook, entered the river on the eastern bank about 750 m downstream of the power station outfalls. Early surveys showed that the very small amounts of sewage and industrial site drainage associated with this stream had little biological effect on the main river downstream, as dilution was high. Full details of the sites and methods were given by Langford (1971) and Langford and Daffern (1975).

To maximize species richness, invertebrates were sampled using three methods: in-stream substrate samples using hand nets with mesh sizes of 0.9 mm (coarse, C) and 250 µm (fine, F) and marginal vegetation samples (marginal, M) (Langford, 1971). Each in-stream substrate sample comprised 3 to 5 kicks at each site. The same number of kicks was used at each site on comparable sampling occasions. The location of in-stream (F and C) and marginal (M) samples at each site were selected haphazardly within an area of approximately 20 m x 20 m and included the major microhabitats (e.g. stones/cobbles, *Ranunculus* sp. vegetation). The river margins were lined with trailing vegetation. Collections using the different methods (coarse, fine or marginal) from the same site and same collection day were sometimes pooled to form fine and marginal (FM), fine and coarse (FC) or fine, coarse and marginal (FCM) samples. Samples were preserved using 2% formalin and organisms identified to the finest possible taxonomic level using the keys available at the time, exceptions being Oligochaeta, Chironomidae, Nematoda and Collembola. Further individuals of the subfamily Orthocladiinae were assigned to two nominate groups (species A and B) based on appearance rather than taxonomic identity. Very small individuals of some species were unidentifiable and, to avoid double counting in richness and diversity indices, counts from several species were combined at family or other higher taxonomic levels (see Supplemental Information 1). Although families may contain species with varying thermal and pollution tolerances, this level of classification is widely used for biological surveillance in England and Wales (Wright et al., 2000).

Quantitative analysis

Of the 232 separate samples, only a comparable subset was used in this study. Samples were restricted to those collected between 1965 and 1971 (see Supplemental Table 1). Only one sample was collected using combined fine and marginal methods (FM) and was therefore removed. This resulted in a data set of 204 samples: 76 at Abbey Bridge, 66 at Garage Bend and 62 at Gasholder. The data represent previously unpublished records and are archived in the Special Collections at the University of Southampton, Hartley Library.

Temperature

To test whether there was a significant difference in the water temperature regime between the sampling sites, three candidate Additive Models were fitted. Five single-spot water temperature measurements were taken at each site using a mercury in glass thermometer within the area sampled for invertebrates. These were represented as a single water temperature measurement as mixing was complete and no detectable variation was found either vertically or horizontally. Sampling at Gasholder and Garage Bend (both temperature and invertebrates) generally coincided with peak downstream temperatures determined using a thermograph at Gasholder. Data used spanned the 1965-1971 sampling period. As samples were taken irregularly and sampling effort varied between years, interannual variability was not included in the models. The models first examined whether there was a relationship between water temperature and day of the year (DOY), and secondly whether the mean value of the relationship between water temperature and DOY was different between sites, or thirdly whether the shape of the relationship between water temperature and DOY varied between sites. The models were fitted using a penalized regression spline from the ‘mgcv’ package in R (Wood, 2003, 2004) which uses cross-validation to determine the amount of smoothing (Zuur, 2012). A cubic regression spline was used for the smoother, as high values of DOY are similar to small values of DOY. The candidate model with the lowest Akaike Information Criterion (AIC) values was selected as the final model. The assumptions of normality, homogeneity of variance and independence were assessed by examining plots of the residuals against the fitted values and covariates. The final model violated the assumption of homogeneity of variance, and was refitted using Generalized Additive Mixed Models with a variety of variance structures (see Zuur et al., 2009), the variance structure that produced the lowest AIC selected.

Community components

Magurran and Henderson (2003) showed that species within a community could be separated into two components (‘core’ and ‘occasional’) based on their abundance and persistence. To examine changes in abundance and taxa richness of these two components a similar approach was used. The whole community of this section of the River Severn was split into groups based on the number of samples a species was recorded in and its abundance ($\log_e$ transformed). The number of groups was determined *a priori* to match Magurran and Henderson's (2003) two 'core' and 'occasional' components. Grouping was carried out using k-means clustering (Hartigan & Wong, 1979).

Abundance, richness and Shannon-Wiener diversity

The impact of the thermal discharge on the community structure was assessed by examining between site differences in Shannon-Wiener diversity, abundance and taxa richness. Changes in both abundance and taxa richness were examined across four metrics: taxa richness and abundance of the whole sample (further referred to as 'total abundance' and 'total richness'), Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa and 'core' and 'occasional' species determined from the k-means clustering. EPT taxa have been shown to be sensitive to anthropogenic disturbance and are often used as an indicator group for pollution assessments (e.g., Lenat, 1988; Baker & Sharp, 1998).

To determine whether the sample metrics differed between sites and with changes in water temperature and DOY, (Generalized) Linear Mixed-Effects Models ((G)LMM) were fitted. One (G)LMM was fitted for each of the nine metrics following a series of methodological steps (see Supplemental Figure 1). Owing to differences in the form of the response variables, the (G)LMMs were fitted using different distributions (Table 1). For the taxa richness metric (positive only integers), initial exploratory analysis tested for overdispersion and either Poisson or negative binomial GLMMs were fitted (Table 1). Model selection followed the protocol suggested by Zuur et al. (2009), whereby an initial model containing all the explanatory variables (e.g. sampling site, water temperature and DOY) and their interactions was fitted, the optimal random structure was identified and then the optimal fixed structure was determined. As effort was consistent across methods, all fine, coarse and marginal samples consisted of the same number of kicks, pooled samples (e.g., FC and FCM) represent increased effort. Community metrics would therefore be potentially more similar within sampling methods in comparison to between sampling methods (e.g., F vs. FCM). To balance this disparity it was determined whether the models required a random effect to be included. As the effect of sampling method was not the focus of the study, the incorporation of a random effect allows the findings to be generalized across sampling approaches (Bolker et al., 2009; Zuur et al., 2009). Plots of the initial model residuals showed differences between sampling method (e.g., F, C, M, FC or FCM) suggesting the incorporation of random effects was warranted. The model assumptions of independence and homogeneity of variance were assessed by examining histograms of the residuals and the residuals plotted against the fitted values and covariates (Zuur et al., 2010). The model fitted to the Shannon-Wiener diversity metric violated the assumption of homogeneity, therefore models incorporating a variety of variance structures were fitted (see Zuur et al., 2009), with the structure producing the lowest AIC value selected. The optimal fixed structure was tested using nested models, whereby more complex models were sequentially tested against models with a variable or interaction removed (Zuur et al., 2009). The ability to drop interaction or main effect terms was assessed by using likelihood ratio tests (normal distribution) or testing the difference in deviance (Poisson and negative binomial) between the nested models. Where there was more than one significant main effect, significance was assessed using a Wald statistic computed from the ‘car’ package (Fox & Weisberg, 2011). Post-hoc tests for the main effects of site, where applicable, were calculated using the ‘multcomp’ package (Hothorn et al., 2008). The (G)LMMs were fitted using the ‘nlme’ (normal distribution; Pinheiro et al., 2013) and ‘glmmADMB’ (Poisson and negative binomial) (Fournier et al., 2012; Skaug et al., 2013) packages in R (version 3.03; R Core Team 2014), with significance assessed at α < 0.01.

Indicator species

To determine whether certain taxa showed an affinity to individual sampling sites, indicator species analysis was undertaken using the 'indicspecies' package (De Cáceres & Legendre, 2009). The default 'indicator value index' which contains a correction for unequal group sizes (Dufrêne & Legendre, 1997) was used to calculate the association between the taxa and the sampling sites. The indicator value index is the combination of the 'specificity' or 'positive predictive value' (A) and the 'fidelity' or 'sensitivity' of the species (B) (Dufrêne & Legendre, 1997). A value of A = 1 would denote that the species/taxon is only found in that group, whereas B = 1 signifies that the species/taxon is present in every sample for that group. Association was calculated from the three individual sampling sites and Garage Bend and Gasholder combined (see De Cáceres et al., 2010). For all tests, analysis was carried out in R (version 3.03; R Core Team 2014), significance was assessed at α < 0.01.

Results

Temperature

The temperature recorded at the sampling sites showed a clear relationship with the day of the year (DOY) on which it was recorded (Fig. 2). Of the three candidate models the one which did not allow the shape of the relationship between DOY and temperature to vary at the different sampling sites had the lowest AIC and was therefore selected as the final model. Examination of the model residuals suggests a violation of the assumption of homogeneity and therefore the model was refitted with a combined variance structure that allowed different variances at the different sampling sites and power of the variance covariate for DOY. The final model suggested water temperature was significantly related to DOY ($F_{6.108, 127.892} = 193.8$, $P < 0.001$) and was significantly different between sites ($F_{2, 132} = 82.36$, $P < 0.001$), with the temperatures at Gasholder and Garage Bend approximately equivalent and on average 4.5°C higher than Abbey Bridge (Fig. 2). The final model explains 91.8 % of the variance in temperature.

Community components

Across the 204 samples a total of 377,204 individuals from 133 taxonomic groups were recorded. The k-means clustering split the community into 30 ‘core’ and 103 ‘occasional’ taxa (Fig. 3). There was an overlap in terms of total abundance between the occasional (n = 1 – 5,316) and core (n = 432 – 101,856) groups. However, the split between the groupings occurred at presence within approximately 80 samples.

Abundance, richness and Shannon-Wiener diversity

The results of the (G)LMMs for the nine sample metrics showed a varied response to the presence of the power station thermal outfall (Table 1). None of the models contained any interaction terms and significance of the main effects varied between models. Of the patterns that were apparent, several of the measures of abundance were significantly different between sites, with generally higher abundance (total, core and occasional) at Abbey Bridge compared with Garage Bend; abundance of occasional taxa was also reduced at Gasholder in comparison to Abbey Bridge. Richness of occasional taxa was significantly reduced at the Garage Bend site in comparison to the upstream control (Abbey Bridge). Occasional taxa abundance and EPT abundance increased with increasing temperature, while the EPT richness increased through the year. The total sample richness, the number of core species recorded per sample, and the Shannon-Wiener statistic for each sample were equal across sampling sites and also had no significant relationship with water temperature or DOY.

Indicator species

Of the 133 taxonomic groups, *Gammarus pulex* (Linnaeus), Orthodadiinae (species A) and Oligochaeta were the most abundant (> 40,000 individuals total across samples) and also recorded in the greatest number of samples. Two species of Simuliidae, *Simulium lineatum* (Meigen) and *S. reptans* var. *galereatum* were also highly abundant as were several EPT taxa, *Serratella ignita* (Poda), Hydropsyche spp., Caenidae spp. and *Psychomyia pusilla* (Fabricius). A number of taxa were restricted to collections from a particular site, with the number of unique taxa higher at Abbey Bridge (n = 14) in comparison with Garage Bend (n =4) or Gasholder (n = 4) (Supplemental Table 2). However, these taxa were generally in very low numbers or infrequently recorded (number of samples < 5), the only exception being Orthocladiinae species B which was recorded on 16 occasions at Abbey Bridge.

The indicator species analysis suggested 11 taxa that were significantly associated with individual sites or the combination of Gasholder and Garage Bend (Table 2). Of the indicator taxa only Orthocladiinae (species B) was restricted to its group (1,414 individuals only at Abbey Bridge), positive predictive value A = 1, and no taxa were recorded in every sample from a group, sensitivity of the species B = 1. *Musculium lacustre* (O. F. Müller) was the species most associated with Abbey Bridge; it was recorded on 41 occasions (2,048 individuals) at Abbey Bridge but only three times at Gasholder (one sample of 760 individuals, 766 total) and was absent from Garage Bend. *Simulium reptans* (Linnaeus) was also more regularly recorded at Abbey Bridge (n = 27; 3,378 individuals), compared with Gasholder and Garage Bend (n = 6; 180 individuals and n = 6; 18 individuals, respectively). *Leuctra moselyi* (Morton) was also regularly recorded at Abbey Bridge but was generally low in abundance across all samples (22 individuals). There was only a single indicator species for Garage Bend, *Sericostoma personatum* (Spence). *S. personatum* was absent from Abbey Bridge but recorded in seven samples at Garage Bend (69 individuals) and two samples at Gasholder (2 individuals). Two Trichoptera, Hydroptila spp. and *Rhyacophila fasciata* (Hagen) were significantly associated with the Gasholder site. While Hydroptila spp. were recorded reasonably regularly at the three sites (11 – 22 records) they were far more abundant at Gasholder. *Rhyacophila fasciata* was encountered in 11 samples at Gasholder compared with five at Garage Bend and a single record from Abbey Bridge, but in low overall abundance (33 individuals). For the combined Gasholder and Garage Bend group, five species were highlighted as potential indicators (Table 2). The species *Asellus aquaticus* (Linnaeus) (mean sample abundance AB = 2.5, GB = 10.4, GH = 13.5), *Sphaerium corneum* (Linnaeus) (AB = 7.0, GB = 24.3, GH = 43.5), *Bithynia tentaculata* (Linnaeus) (AB = 6.9, GB = 18.6, GH = 28.2), *Limnius volckmari* (Panzer) (AB = 6.4, GB = 8.3, GH = 15.5) and *Erpobdella octoculata* (Linnaeus) (AB = 1.5, GB = 3.0, GH = 8.1), were generally abundant or recorded regularly being within the ‘core’ group; however, abundance was lowest at Abbey Bridge, then higher at Garage Bend and higher still at Gasholder.

Discussion

The macro-invertebrate community downstream of Ironbridge ‘A’ power station showed a varied response to the higher water temperatures. There was evidence of higher invertebrate abundance at the control site, Abbey Bridge, in comparison to the site closest to the thermal discharge (Garage Bend). This reduction in abundance was evident in all the metrics used (total abundance, and abundance of core, occasional and EPT taxa); however, samples taken at Gasholder (2 km downstream of the outfall) were generally similar to samples from the control site in terms of the metrics considered. Due to the lack of replicated sites it is difficult to separate changes in the community metrics in relation to increased water temperature as opposed to river habitat variability. However, two potential mechanisms may explain the observed patterns in abundance. Firstly, slight differences in the physical structure of the river at the different sampling site may produce different assemblages. For example, the Garage Bend site was slightly deeper and less turbulent than the other sampling locations, while the presence of brick and tile debris at Gasholder (see Table 1; Langford, 1971), may have altered community composition. Secondly, water temperatures measured on the day of sampling may not adequately capture the impact of historic changes in thermal regime. Although the water temperatures were very similar at Gasholder and Garage Bend (Fig. 2) and approximately 4.5°C higher than Abbey Bridge, the maximum temperature rise at the downstream sites could be as great as 8°C (Langford, 1970). Further, the highest temperature recorded was measured about 150 m downstream of the outfall (31.8°C; Langford, *unpublished data*). River temperature rise was also related to power station operation which was reduced both in power output and number of operating hours during the study compared to historic levels (Langford, 1970). It is likely therefore that downstream temperatures had historically been higher and lasted for longer periods, and thus some residual effect of the disturbance history (e.g., Harding et al., 1998; Foster et al., 2003, for land use) may have impacted the Garage Bend site as it was closer to the outfall. Differences in EPT abundance between sites contradict the findings of Langford (1971) who examined Trichoptera and Plecoptera abundance in the same reach of the River Severn. This disparity may be explained by differences in the timing of study, the statistical approach or the combined EPT metrics used in this study.

Decreases in abundance would mirror findings from both field studies and experimental manipulations. A 2 – 3.5°C increase in water temperature resulted in reduced invertebrate densities (Hogg et al., 1995; Hogg & Williams, 1996). Hogg and Williams (1996) suggest such reductions in abundance/density may be a product of increased respiration to production ratios leading to reduced resource use efficiency within the stream systems. Similarly, predictions for small river systems in Wales suggest that temperature increases of *ca.* 1°C may result in reduction in the springtime abundance of some macro-invertebrates (Durance & Ormerod, 2007). Drawing definitive parallels between the previously highlighted studies and our analysis is somewhat reduced by differences in the thermal regime of the study locations. For example, the spring-fed stream of the Hogg and Williams (1996) and Hogg et al. (1995) studies is likely to have a less variable thermal regime and therefore may be more impacted by temperature increases. Conversely, small upland streams in Wales (e.g. Durance & Ormerod, 2007) may show greater natural temperature fluctuations than the larger River Severn. However, the diurnal variations downstream of the power station were comparable with the regime of small streams, while the unaffected reaches upstream show very little diurnal temperature variation (Langford, 1970). Reduced total invertebrate abundance may impact energy transfer through the food web, potentially limiting resource availability for predatory species (Durance & Ormerod, 2007). Differences in abundance should be viewed with caution because of the use of hand net kick and sweep sampling which can be variable whether timed or areal sampling is used (Frost et al., 1971; Furse et al., 1981).

The absence of a negative relationship between any of the metrics and the water temperature recorded during the sampling event suggests that during the study period taxa did not reach their critical thermal maxima. As previously stated, there are limitations in the temperature record available for the reach, as spot temperatures may not accurately capture the thermal history of the site. In contrast to a decline, both occasional and EPT taxa abundance increased with elevated temperature. This result is likely driven by life history strategies, with egg incubation period in Ephemeroptera, Plecoptera and Trichoptera being highly influenced by temperature (Brittain, 1977, 1990). Most species recorded in this section of the River Severn are at maximum abundance in summer. The increase in EPT and occasional taxa abundance with temperature, in reality, as opposed to the current model, is unlikely to be linear while with increasing temperature, aquatic species may face ‘oxygen squeeze’ as available oxygen deceases while biological oxygen demand increases (Ficke et al., 2007). The response of species to climate change is likely to be highly taxon-specific: Haidekker and Hering (2008) found an almost equal positive/negative split in the correlation between EPT (and Coleoptera) taxa abundance and summer mean temperature. Despite this lack of a consistent trend, species with certain traits (Poff et al., 2010; Diamond et al., 2011; Conti et al., 2014) or from specific taxonomic groups (e.g., Plecoptera) (Haidekker & Hering, 2008), may respond in a similar manner.

Despite the thermal impact, taxonomic richness overall and for the 'core' group was similar across sites. Conversely, 'occasional' and EPT taxa richness was reduced at the thermally impacted Garage Bend site. The occasional group also contained a number of taxa that could be described as rare transients, with only a few or even single individuals recorded on a very few occasions (e.g., *Brachycercus harrisella*, Curtis, and *Ecdyonurus dispar*, Curtis). The absence of a response from taxa within these groups at the Gasholder site (which was also subject to similarly elevated temperatures) is, as with the abundance metrics, likely related to either habitat variation, lack of resolution on the temperature monitoring, or legacy effects of historic power station operation. Changes in taxa richness have been noted in other communities associated with thermal discharges, although the magnitude of the temperature increase was often greater (e.g., Poff & Matthews, 1986; Langford, 1990; Wellborn & Robinson, 1996). In other studies, reduced diversity may have been more related to chlorine use for anti-fouling than effects of temperature (see Langford 1990). However, in this study, because of the distance downstream from the outfall, the very small amounts of chlorine used at the Ironbridge 'A' power station (target 0.02 mgL^{-1} at the outfall) chlorine decay was complete at Garage Bend and Gasholder. The trajectory (increase or decrease) of temperature-mediated changes in taxonomic richness will depend on the species' physiological tolerances (Woodward et al., 2010). In field simulations, taxonomic richness remained constant with water temperature increases of 3.5 – 6.5°C (Hogg & Williams, 1996; Tixier et al., 2009). Bioclimatic envelope models also predict that suitable climatic conditions will still persist for the vast majority of European stream macro-invertebrates in the year 2080 (Domisch et al., 2013).

While diversity, richness and abundance provide useful overall metrics, they fail to recognize changes in assemblage taxonomic composition. For example, richness may remain static in relation to disturbance despite a shift in community composition from specialist to generalist species (e.g., Freeman & Marcinek, 2006; Hering et al., 2009). To address this issue, indicator species analysis was used to highlight taxa that showed an association with a particular site or group of sites. Four taxa were significantly associated with the Abbey Bridge site, *M. lacustre, S. reptans*, Orthocladiinae species B and *L. moselyi*. Orthocladiinae species B was the only taxon present at this site and was both recorded reasonably regularly and in high abundance. Orthocladiinae have been described as cold-stenothermal (Hoang et al., 2006), with abundance of certain subfamilies reduced by temperature rises in experimental manipulations (Nordlie & Arthur, 1981). Unlike the present study, density of the blackfly larvae *S. reptans* was not significantly related to temperature in the Nemunas River, Lithuania (Bernotiene, in press). Climate warming and an extreme heatwave reduced richness and abundance of mollusc communities in the Saône River, France; however *M. lacustre* was more resilient to these changes (Mouthon & Daufresne, 2006). In contrast to the findings of this study, this species is thought to tolerate high summer temperatures and may become the dominant sphaeriid species in response to climate warming (Mouthon, 2004). The fourth indicator species, *L. moselyi*, has been shown to have low egg hatching success at temperatures around 20°C (Elliott, 1987), which may explain its association with the colder water site in the present study. However, in contrast to our study, *L. moselyi* was shown to be associated with warmer years in upland streams in the UK (Durance & Ormerod, 2007). It should be noted that *L. moselyi* was generally recorded in low numbers in our study and therefore inference should be treated with caution.

Three taxa, *S. personatum* (Garage Bend), Hydroptila spp. and *R. fasciata* (Gasholder) were significantly associated with the thermally impacted sites. The association of *S. personatum* with the site closest to the thermal discharge is surprising given that high temperature has been suggested as a factor limiting its occurrence (Friberg & Jacobsen, 1999). In line with the greater abundances observed at Gasholder, *Hydroptila* abundance was approximately doubled in an experimental channel subject to increased temperatures of 10°C (Nordlie & Arthur, 1981). Distribution of *R. fasciata* was found to have little relationship to water temperature in a Slovenian karst river (Hrovat & Urbanic, 2012); however, low overall abundance in our study suggests the association of this species with the Garage Bend site should be treated with caution.

Five species were significantly associated with the Garage Bend and Gasholder sites combined. All five of these species were members of the core taxa grouping and were therefore generally abundant and while they were regularly recorded at Abbey Bridge, abundances were reduced at that site. *A. aquaticus*, a common species at the downstream sites at Ironbridge, can acclimate to increased temperatures (Korhonen & Lagerspetz, 1996) while also being able to regulate oxygen uptake (Rotvit & Jacobsen, 2013). In response to elevated temperatures associated with power station discharges, *A. aquaticus* can also exhibit a reduced life cycle length (Aston & Milner, 1980; Langford, 1990). Similarly, *E. octoculata* were also significantly more abundant at Gasholder and Garage Bend than at Abbey Bridge; *E. octoculata* are generally considered to be tolerant to different types of anthropogenic pollution and this observation is consistent with the findings of Fey (1977) who observed an increased abundance of *E. octoculata* downstream of the Elverslingen power station on the River Lenne, Germany. *E. octoculata* was also common in the River Trent despite the river suffering the combined effects of gross domestic sewage pollution and increases in temperature due to the presence of multiple power stations (Aston & Brown, 1975). *L. volckmari* was also more abundant at the warmwater sites matching a study in small and medium-sized streams in Germany which found this species was positively correlated with summer mean temperature (Haidekker & Hering, 2008). *B. tentaculata* was present in greater numbers at Gasholder and Garage Bend than Abbey Bridge; this may be linked to the species' ability to undertake metabolic depression to acclimate to or survive unfavourable conditions (Hahn, 2005). In streams in eastern Turkey abundance of *B. tentaculata* was also positively related to temperature (Sahin, 2012).

Climate change is projected to be one of the greatest threats to freshwater biodiversity (Sala et al., 2000). As the average temperature increases because of the effect of the power station were consistent or above those predicted due to climate change, this study may provide an indication of the possible response of benthic macro-invertebrates to future river temperature regimes. Detecting climate change responses has generally focused on individual species responses or controlled laboratory/mesocosm experiments (see Woodward et al., 2010). Whilst studies such as this in the River Severn capture more of the complexity in natural systems, issues related to replication and variation in underlying physicochemical conditions can make drawing clear conclusions challenging (Woodward et al., 2010). A limitation of the water temperature data used in this analysis is the temporally consistent increase in temperature downstream of the power station (Fig. 2). Climate change projections suggest greater intra-annual variability with larger temperature increases during summer months (Jenkins et al., 2009). This intra-annual variability will impact species differently depending on their life history traits, e.g. timing of growth or reproduction.

Overall, this study suggests that the altered temperature regime downstream of the Ironbridge ‘A’ power station had a measurable impact on parts of the macro-invertebrate community in the River Severn at this location. Measured abundances and richness were reduced at the site closest to the power station outfall; however, these metrics were not affected at the second thermally disturbed site further downstream. In essence, there were winners and losers (see also Domisch et al., 2011; Floury et al., 2013), with tolerant taxa e.g. *A. aquaticus* and *E. octoculata* showing increased abundance in the heated reach, with a reduction in Orthocladiinae numbers. Such results are reported consistently in studies of impacts of temperature perturbations on macro-invertebrates both due to power stations and the effects of climatic change (see Daufresne et al., 2004; Chessman, 2009). In the current study the majority of macro-invertebrates were present at both elevated and ambient temperatures; therefore the majority of taxa were likely not at their critical thermal tolerance threshold or could adapt their behaviour to deal with higher temperatures. Temperature increases of the magnitude recorded in this study appear unlikely to result in reduced taxonomic diversity, although some change in community composition may occur.

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Tables

Table 1 Results of the (Generalized) Linear Mixed-Effects Models showing the distribution used and whether a random intercept for sampling method was required. Test statistics for significant main effects and post-hoc tests between sampling sites presented. Figures in bold represent statistical significance at α < 0.01.

Metric	Distribution	Random Intercept	Day of the Year	Water Temperature	Site	AB = GB	AB = GH	GB = GH
Total Abundance	Normal	✓	–	–	**$F_{2,197}$ = 7.75, *P* < 0.001**	**z =-3.83, *P* < 0.001**	z = -0.93, *P* = 0.62	z =2.73, *P* = 0.017
Total Richness	Negative Binomial	✓	–	–	–	–	–	–
Core Abundance	Normal	✓	–	–	**$F_{2,197}$ = 7.46, *P* < 0.001**	**z =-3.68, *P* < 0.001**	z = -0.64, *P* = 0.80	z =2.88, *P* = 0.011
Core Richness	Poisson	✓	–	–	–	–	–	–
Occasional	Normal	✓	–	**χ^2 = 13.21, 1 d.f.,**	**χ^2 = 30.21, 2 d.f.,**	**z =-5.06,**	**z =-4.43,**	z = 0.62,

Abundance[a]				**$P < 0.001$**	**$P < 0.001$**	**$P < 0.001$**	**$P < 0.001$**	$P = 0.81$
Occasional Richness	Negative Binomial	✓	–	–	**χ2= 11.41, 2 d.f.,** **$P = 0.003$**	**$z = -2.96$,** **$P = 0.008$**	$z = -1.58$, $P = 0.24$	$z = 0.98$, $P = 0.57$
EPT Abundance	Normal	✓	–	**$\chi^2 = 20.96$, 1 d.f.,** **$P < 0.001$**	**$\chi^2 = 21.41$, 2 d.f.,** **$P < 0.001$**	**$z = -4.52$,** **$P < 0.001$**	$z = -1.47$, $P = 0.31$	**$z = 3.05$,** **$P = 0.006$**
EPT Richness[b]	Poisson	✓	**$\chi^2 = 9.47$, 1 d.f.,** **$P = 0.002$**	–	$\chi^2 = 6.16$, 2 d.f., $P = 0.046$	$z = -2.48$, $P = 0.033$	$z = -0.06$, $P = 1.0$	$z = 1.74$, $P = 0.18$
Shannon-Wiener[c]	Normal	✓	–	–	–	–	–	–

a. Based on examination of residual plots an outlier was removed and models re-run.

b. Examination of residuals versus sampling site suggested violation of the assumption of homogeneity, therefore site included in final model.

c. Model fitted with a power of the covariate variance structure for the day of the year across different strata (sampling sites).

Table 2 Results from indicator species analysis showing the taxa significantly associated with the three individual sampling sites and the combination of Gasholder and Garage Bend. The two components of the indicator species analysis are shown: positive predictive value (A) and sensitivity of the species (B). The results of the indicator species analysis in relation to published literature are shown; taxa that were quoted as having no significant relationship to temperature in the literature are denoted by NS.

Species	**A**	**B**	**Statistic**	**P value**	**Match to Literature**	**Reference(s)**
Abbey Bridge						
Musculium lacustre	0.69	0.54	0.61	0.001	NS	Mouthon, 2004
Simulium reptans	0.94	0.36	0.58	0.001	No	Bernotiene, in press
Orthocladiinae Species B	1.00	0.21	0.46	0.001	Yes	Nordlie & Arthur, 1981; Hoang et al., 2006
Leuctra moselyi	0.84	0.11	0.30	0.010	No/Yes	Elliott, 1987; Durance & Ormerod, 2007
Garage Bend						
Sericostoma personatum	0.97	0.11	0.32	0.005	No	Friberg & Jacobsen, 1999
Gasholder						
Hydroptila spp.	0.79	0.35	0.53	0.005	Yes	Nordlie & Arthur, 1981
Rhyacophila fasciata	0.80	0.18	0.38	0.002	NS	Hrovat & Urbanic, 2012

Gasholder and Garage Bend						
Asellus aquaticus	0.91	0.80	0.85	0.001	Yes	Korhonen & Lagerspetz, 1996
Sphaerium corneum	0.91	0.69	0.79	0.001		
Bithynia tentaculata	0.87	0.71	0.79	0.004	Yes	Sahin, 2012
Limnius volckmari	0.79	0.73	0.76	0.005	Yes	Haidekker & Hering, 2008
Erpobdella octoculata	0.88	0.65	0.76	0.001	Yes	Aston & Brown, 1975; Fey, 1977

Figure captions

Fig. 1 Location of Abbey Bridge, Garage Bend and Gasholder sampling stations in relation to Ironbridge “A” power station (redrawn from Langford, 1970)

Fig. 2 The relationship between water temperature and day of the year for the three sampling sites. Temperature was significantly higher for Garage Bend (solid line, solid triangles) and Gasholder (dotted line, open circles) compared to Abbey Bridge (dashed line, solid circles). Note: The lines for Garage Bend and Gasholder overlap and are thus difficult to distinguish

Fig. 3 The number of samples taxon were recorded in, versus their total abundance. Taxa split into ‘occasional’ (open circles) and ‘core’ (solid triangles) components based on k-means clustering