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

3

4 T. A. Worthington ^{a, b, c *}, P.J. Shaw ^b, J.R. Daffern ^d and T.E.L. Langford ^b

5

6 ^a Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State University,
7 Stillwater, Oklahoma 74078, USA

8

9 ^b Faculty of Engineering and the Environment, University of Southampton, Highfield,
10 Southampton SO17 1BJ, UK

11

12 ^c Department of Biology, University of Maryland (Visiting Researcher), College Park,
13 Maryland 20742, USA

14

15 ^d 4 Menevia Grove, Presteigne, Powys LD8 2LP, UK

16

17 * Corresponding author: thomas.worthington@okstate.edu, Telephone: (405) 744-6342;

18 Fax: (405) 744-5006

19

20 **Abstract**

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

38

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

41

42 **Introduction**

43

44 Human activities have severely degraded many of the world's freshwater systems,
45 particularly rivers, over many years (e.g., Hawkes, 1956; Hynes, 1960; Revenga et al., 2000),
46 with recent rapid human population growth increasing the stress on global water resources
47 (Duda & El-Ashry, 2000). The combination of multiple stressors, including pollution, habitat
48 fragmentation and loss, land-use changes, and over-exploitation, has resulted in declines of
49 many indigenous species and relatively high extinction rates for freshwater organisms
50 (Ricciardi & Rasmussen, 1999; Revenga et al., 2000; Jenkins, 2003; Dudgeon et al., 2006).

51 Temperature is considered one of the most important physical influences on both the
52 composition of macro-invertebrate communities and on phenology of individual species
53 (Hynes, 1960; Langford, 1990). Among the many anthropogenic activities which have
54 directly or indirectly caused changes in river temperatures and aquatic biota are tree-
55 clearance, impoundments and thermal discharges from power stations and other industries
56 (Langford, 1983, 1990; Caissie, 2006; Broadmeadow, et al. 2011).

57 Since the late 19th century, global average air temperatures have increased by
58 almost 0.8°C (Jenkins et al., 2008) and are projected to rise further (Bates et al., 2008; IPCC,
59 2013). Temperatures of some UK rivers indicate warming over the last 20 to 30 years
60 (Hammond & Pryce, 2007), although the closure of direct-cooled power stations has
61 resulted in cooling of certain reaches (Langford et al., 2012). Summer temperatures in some
62 UK river systems are predicted to rise by up to 4°C (Johnson et al., 2009), while changes in
63 precipitation and evapotranspiration are expected to increase the frequency of drought and
64 flood episodes (Hulme et al., 2002; Wilby et al., 2010; Watts et al., 2013). Due to the
65 relationship between climate patterns and fluvial processes and the interaction with other

66 stressors, freshwater environments are considered to be some of the systems most
67 sensitive to climate change (Durance & Ormerod, 2009).

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

80 At the community level, thermal discharges from power station outfalls have been
81 associated with changes in composition such as a reduction in the abundance of
82 temperature-sensitive species (Obrdlík et al., 1979), an increase in the abundance of
83 temperature-tolerant taxa (Aston, 1973), reduced standing crop (Durrett & Pearson, 1975),
84 and the creation of conditions suitable for non-native species (Howells, 1983). In addition to
85 a higher risk of mortality for temperature-sensitive taxa (e.g., Dallas & Ketley, 2011),
86 temperature increases are also thought to affect species phenology in the form of reduced
87 life cycle length and earlier hatching and emergence (Langford, 1971; Langford & Daffern,
88 1975; Aston & Milner, 1980).

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

95

96 **Materials and methods**

97

98 Site characteristics and sampling

99

100 The study was carried out in the vicinity of the Ironbridge 'A' power station on the upper-
101 middle reaches of the River Severn, UK (Fig. 1). This reach was selected because of the lack
102 of upstream industrial pollution, high macro-invertebrate diversity and the presence of
103 many pollution-sensitive taxa (Langford & Daffern, 1975). Also, the power station used a
104 large proportion of the river flow during periods of low discharge resulting in high
105 downstream temperatures, while there was little trace of chlorine or other anti-foulants
106 which can complicate thermal discharge effects in more polluted rivers (Langford, 1970,
107 1971). The River Severn is the longest river in the UK, rising in the Cambrian Mountains,
108 Wales (headwaters 741m above Ordnance Datum), flowing east then south for 354km until
109 it reaches the Bristol Channel (Jones et al., 2012). In the Ironbridge area the River Severn
110 alternates between slow deep reaches and short riffles as it passes through the Ironbridge
111 Gorge (Langford, 1970, 1971). Water chemistry measurements upstream and downstream
112 recorded dissolved oxygen (mg l^{-1}) 9.2–14.8, ammonia ($\text{NH}_3 \text{ mg l}^{-1}$) 0–0.94 and pH 7.6–8.4,

113 and were similar between the two sites (Langford, 1971). Ironbridge 'A' power station was
114 commissioned in 1932 and had a maximum potential output of 210 MW. The station
115 consisted of four direct-cooled generating units, with $15.2 \text{ m}^3\text{s}^{-1}$ of river water being passed
116 through the cooling system at peak output. During the study period, Ironbridge 'A' was
117 operating for approximately 15–17 hours per day and water usage could exceed more than
118 50% of the river flow in low discharge periods. Depending on the extent of power
119 generation and the river discharge, the thermal discharge resulted in increases of up to 8°C
120 at the downstream sampling sites used in this analysis, with elevated temperatures ($+5^\circ\text{C}$)
121 recorded up to 5 km downstream of the power station (Langford, 1970). Maximum
122 temperatures during the period 1965-75 were 22°C at the upstream sampling site and
123 29.5°C at the downstream site. The maximum effluent temperature in the same period was
124 31.5°C measured 50 m downstream of the outfalls (Langford, *unpublished data*). Diurnal
125 variation contrasted between the sites with upstream daily temperature fluctuations
126 confined to periods of very high air temperatures or very low flows. Downstream of the
127 power station, temperature peaks occurred during the middle of the day, in response to
128 power station activity (Langford, 1970). There was no measurable thermal stratification at
129 the downstream site, indicating that the river water had been completely mixed with the
130 power station effluent 2 km downstream of the outfall (Langford, 1970).

131 Over the period of June 1965 to May 1984 a total of 232 separate macro-
132 invertebrate samples were taken from in-stream and marginal habitats. Invertebrate
133 sampling was carried out at three survey sites: Abbey Bridge (AB; 500 m upstream of the
134 Ironbridge 'A' outfall), Garage Bend (GB; 600 m below the outfall) and Gasholder (GH; 2 km
135 below the outfall). The physical characteristics of the river at the three survey sites were
136 broadly similar, being fast-flowing riffles (Langford, 1971; Langford & Daffern, 1975), though

137 the Garage Bend site was slightly deeper than the other two sites. Substrate composition at
138 the three sites generally comprised coarse sand overlain with limestone cobbles (3–25 cm);
139 in addition there was some brick and tile debris from demolished furnaces at the Gasholder
140 site (Langford, 1971). A small, historically polluted stream, the Coalbrook, entered the river
141 on the eastern bank about 750 m downstream of the power station outfalls. Early surveys
142 showed that the very small amounts of sewage and industrial site drainage associated with
143 this stream had little biological effect on the main river downstream, as dilution was high.
144 Full details of the sites and methods were given by Langford (1971) and Langford and
145 Daffern (1975).

146 To maximize species richness, invertebrates were sampled using three methods: in-
147 stream substrate samples using hand nets with mesh sizes of 0.9 mm (coarse, C) and 250
148 μm (fine, F) and marginal vegetation samples (marginal, M) (Langford, 1971). Each in-stream
149 substrate sample comprised 3 to 5 kicks at each site. The same number of kicks was used at
150 each site on comparable sampling occasions. The location of in-stream (F and C) and
151 marginal (M) samples at each site were selected haphazardly within an area of
152 approximately 20 m x 20 m and included the major microhabitats (e.g. stones/cobbles,
153 *Ranunculus* sp. vegetation). The river margins were lined with trailing vegetation.
154 Collections using the different methods (coarse, fine or marginal) from the same site and
155 same collection day were sometimes pooled to form fine and marginal (FM), fine and coarse
156 (FC) or fine, coarse and marginal (FCM) samples. Samples were preserved using 2% formalin
157 and organisms identified to the finest possible taxonomic level using the keys available at
158 the time, exceptions being Oligochaeta, Chironomidae, Nematoda and Collembola. Further
159 individuals of the subfamily Orthoclaadiinae were assigned to two nominate groups (species
160 A and B) based on appearance rather than taxonomic identity. Very small individuals of

161 some species were unidentifiable and, to avoid double counting in richness and diversity
162 indices, counts from several species were combined at family or other higher taxonomic
163 levels (see Supplemental Information 1). Although families may contain species with varying
164 thermal and pollution tolerances, this level of classification is widely used for biological
165 surveillance in England and Wales (Wright et al., 2000).

166

167 Quantitative analysis

168

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

175

176 *Temperature*

177

178 To test whether there was a significant difference in the water temperature regime
179 between the sampling sites, three candidate Additive Models were fitted. Five single-spot
180 water temperature measurements were taken at each site using a mercury in glass
181 thermometer within the area sampled for invertebrates. These were represented as a single
182 water temperature measurement as mixing was complete and no detectable variation was
183 found either vertically or horizontally. Sampling at Gasholder and Garage Bend (both
184 temperature and invertebrates) generally coincided with peak downstream temperatures

185 determined using a thermograph at Gasholder. Data used spanned the 1965-1971 sampling
186 period. As samples were taken irregularly and sampling effort varied between years,
187 interannual variability was not included in the models. The models first examined whether
188 there was a relationship between water temperature and day of the year (DOY), and
189 secondly whether the mean value of the relationship between water temperature and DOY
190 was different between sites, or thirdly whether the shape of the relationship between water
191 temperature and DOY varied between sites. The models were fitted using a penalized
192 regression spline from the 'mgcv' package in R (Wood, 2003, 2004) which uses cross-
193 validation to determine the amount of smoothing (Zuur, 2012). A cubic regression spline
194 was used for the smoother, as high values of DOY are similar to small values of DOY. The
195 candidate model with the lowest Akaike Information Criterion (AIC) values was selected as
196 the final model. The assumptions of normality, homogeneity of variance and independence
197 were assessed by examining plots of the residuals against the fitted values and covariates.
198 The final model violated the assumption of homogeneity of variance, and was refitted using
199 Generalized Additive Mixed Models with a variety of variance structures (see Zuur et al.,
200 2009), the variance structure that produced the lowest AIC selected.

201

202 *Community components*

203

204 Magurran and Henderson (2003) showed that species within a community could be
205 separated into two components ('core' and 'occasional') based on their abundance and
206 persistence. To examine changes in abundance and taxa richness of these two components
207 a similar approach was used. The whole community of this section of the River Severn was
208 split into groups based on the number of samples a species was recorded in and its

209 abundance (\log_e transformed). The number of groups was determined *a priori* to match
210 Magurran and Henderson's (2003) two 'core' and 'occasional' components. Grouping was
211 carried out using k-means clustering (Hartigan & Wong, 1979).

212

213 *Abundance, richness and Shannon-Wiener diversity*

214

215 The impact of the thermal discharge on the community structure was assessed by examining
216 between site differences in Shannon-Wiener diversity, abundance and taxa richness.

217 Changes in both abundance and taxa richness were examined across four metrics: taxa
218 richness and abundance of the whole sample (further referred to as 'total abundance' and
219 'total richness'), Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa and 'core' and
220 'occasional' species determined from the k-means clustering. EPT taxa have been shown to
221 be sensitive to anthropogenic disturbance and are often used as an indicator group for
222 pollution assessments (e.g., Lenat, 1988; Baker & Sharp, 1998).

223 To determine whether the sample metrics differed between sites and with changes
224 in water temperature and DOY, (Generalized) Linear Mixed-Effects Models ((G)LMM) were
225 fitted. One (G)LMM was fitted for each of the nine metrics following a series of
226 methodological steps (see Supplemental Figure 1). Owing to differences in the form of the
227 response variables, the (G)LMMs were fitted using different distributions (Table 1). For the
228 taxa richness metric (positive only integers), initial exploratory analysis tested for
229 overdispersion and either Poisson or negative binomial GLMMs were fitted (Table 1). Model
230 selection followed the protocol suggested by Zuur et al. (2009), whereby an initial model
231 containing all the explanatory variables (e.g. sampling site, water temperature and DOY) and
232 their interactions was fitted, the optimal random structure was identified and then the

233 optimal fixed structure was determined. As effort was consistent across methods, all fine,
234 coarse and marginal samples consisted of the same number of kicks, pooled samples (e.g.,
235 FC and FCM) represent increased effort. Community metrics would therefore be potentially
236 more similar within sampling methods in comparison to between sampling methods (e.g., F
237 vs. FCM). To balance this disparity it was determined whether the models required a
238 random effect to be included. As the effect of sampling method was not the focus of the
239 study, the incorporation of a random effect allows the findings to be generalized across
240 sampling approaches (Bolker et al., 2009; Zuur et al., 2009). Plots of the initial model
241 residuals showed differences between sampling method (e.g., F, C, M, FC or FCM)
242 suggesting the incorporation of random effects was warranted. The model assumptions of
243 independence and homogeneity of variance were assessed by examining histograms of the
244 residuals and the residuals plotted against the fitted values and covariates (Zuur et al.,
245 2010). The model fitted to the Shannon-Wiener diversity metric violated the assumption of
246 homogeneity, therefore models incorporating a variety of variance structures were fitted
247 (see Zuur et al., 2009), with the structure producing the lowest AIC value selected. The
248 optimal fixed structure was tested using nested models, whereby more complex models
249 were sequentially tested against models with a variable or interaction removed (Zuur et al.,
250 2009). The ability to drop interaction or main effect terms was assessed by using likelihood
251 ratio tests (normal distribution) or testing the difference in deviance (Poisson and negative
252 binomial) between the nested models. Where there was more than one significant main
253 effect, significance was assessed using a Wald statistic computed from the 'car' package
254 (Fox & Weisberg, 2011). Post-hoc tests for the main effects of site, where applicable, were
255 calculated using the 'multcomp' package (Hothorn et al., 2008). The (G)LMMs were fitted
256 using the 'nlme' (normal distribution; Pinheiro et al., 2013) and 'glmmADMB' (Poisson and

257 negative binomial) (Fournier et al., 2012; Skaug et al., 2013) packages in R (version 3.03; R
258 Core Team 2014), with significance assessed at $\alpha < 0.01$.

259

260 *Indicator species*

261

262 To determine whether certain taxa showed an affinity to individual sampling sites, indicator
263 species analysis was undertaken using the 'indicspecies' package (De Cáceres & Legendre,
264 2009). The default 'indicator value index' which contains a correction for unequal group
265 sizes (Dufrêne & Legendre, 1997) was used to calculate the association between the taxa
266 and the sampling sites. The indicator value index is the combination of the 'specificity' or
267 'positive predictive value' (A) and the 'fidelity' or 'sensitivity' of the species (B) (Dufrêne &
268 Legendre, 1997). A value of A = 1 would denote that the species/taxon is only found in that
269 group, whereas B = 1 signifies that the species/taxon is present in every sample for that
270 group. Association was calculated from the three individual sampling sites and Garage Bend
271 and Gasholder combined (see De Cáceres et al., 2010). For all tests, analysis was carried out
272 in R (version 3.03; R Core Team 2014), significance was assessed at $\alpha < 0.01$.

273

274 **Results**

275

276 Temperature

277

278 The temperature recorded at the sampling sites showed a clear relationship with the day of
279 the year (DOY) on which it was recorded (Fig. 2). Of the three candidate models the one
280 which did not allow the shape of the relationship between DOY and temperature to vary at

281 the different sampling sites had the lowest AIC and was therefore selected as the final
282 model. Examination of the model residuals suggests a violation of the assumption of
283 homogeneity and therefore the model was refitted with a combined variance structure that
284 allowed different variances at the different sampling sites and power of the variance
285 covariate for DOY. The final model suggested water temperature was significantly related to
286 DOY ($F_{6,108, 127.892} = 193.8, P < 0.001$) and was significantly different between sites ($F_{2, 132} =$
287 $82.36, P < 0.001$), with the temperatures at Gasholder and Garage Bend approximately
288 equivalent and on average 4.5°C higher than Abbey Bridge (Fig. 2). The final model explains
289 91.8 % of the variance in temperature.

290

291 Community components

292

293 Across the 204 samples a total of 377,204 individuals from 133 taxonomic groups were
294 recorded. The k-means clustering split the community into 30 'core' and 103 'occasional'
295 taxa (Fig. 3). There was an overlap in terms of total abundance between the occasional ($n =$
296 $1 - 5,316$) and core ($n = 432 - 101,856$) groups. However, the split between the groupings
297 occurred at presence within approximately 80 samples.

298

299 Abundance, richness and Shannon-Wiener diversity

300

301 The results of the (G)LMMs for the nine sample metrics showed a varied response to the
302 presence of the power station thermal outfall (Table 1). None of the models contained any
303 interaction terms and significance of the main effects varied between models. Of the
304 patterns that were apparent, several of the measures of abundance were significantly

305 different between sites, with generally higher abundance (total, core and occasional) at
306 Abbey Bridge compared with Garage Bend; abundance of occasional taxa was also reduced
307 at Gasholder in comparison to Abbey Bridge. Richness of occasional taxa was significantly
308 reduced at the Garage Bend site in comparison to the upstream control (Abbey Bridge).
309 Occasional taxa abundance and EPT abundance increased with increasing temperature,
310 while the EPT richness increased through the year. The total sample richness, the number of
311 core species recorded per sample, and the Shannon-Wiener statistic for each sample were
312 equal across sampling sites and also had no significant relationship with water temperature
313 or DOY.

314

315 Indicator species

316

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

327 The indicator species analysis suggested 11 taxa that were significantly associated
328 with individual sites or the combination of Gasholder and Garage Bend (Table 2). Of the

329 indicator taxa only Orthoclaadiinae (species B) was restricted to its group (1,414 individuals
330 only at Abbey Bridge), positive predictive value $A = 1$, and no taxa were recorded in every
331 sample from a group, sensitivity of the species $B = 1$. *Musculium lacustre* (O. F. Müller) was
332 the species most associated with Abbey Bridge; it was recorded on 41 occasions (2,048
333 individuals) at Abbey Bridge but only three times at Gasholder (one sample of 760
334 individuals, 766 total) and was absent from Garage Bend. *Simulium reptans* (Linnaeus) was
335 also more regularly recorded at Abbey Bridge ($n = 27$; 3,378 individuals), compared with
336 Gasholder and Garage Bend ($n = 6$; 180 individuals and $n = 6$; 18 individuals, respectively).
337 *Leuctra moselyi* (Morton) was also regularly recorded at Abbey Bridge but was generally low
338 in abundance across all samples (22 individuals). There was only a single indicator species
339 for Garage Bend, *Sericostoma personatum* (Spence). *S. personatum* was absent from Abbey
340 Bridge but recorded in seven samples at Garage Bend (69 individuals) and two samples at
341 Gasholder (2 individuals). Two Trichoptera, Hydroptila spp. and *Rhyacophila fasciata*
342 (Hagen) were significantly associated with the Gasholder site. While Hydroptila spp. were
343 recorded reasonably regularly at the three sites (11 – 22 records) they were far more
344 abundant at Gasholder. *Rhyacophila fasciata* was encountered in 11 samples at Gasholder
345 compared with five at Garage Bend and a single record from Abbey Bridge, but in low
346 overall abundance (33 individuals). For the combined Gasholder and Garage Bend group,
347 five species were highlighted as potential indicators (Table 2). The species *Asellus aquaticus*
348 (Linnaeus) (mean sample abundance AB = 2.5, GB = 10.4, GH = 13.5), *Sphaerium corneum*
349 (Linnaeus) (AB = 7.0, GB = 24.3, GH = 43.5), *Bithynia tentaculata* (Linnaeus) (AB = 6.9, GB =
350 18.6, GH = 28.2), *Limnius volckmari* (Panzer) (AB = 6.4, GB = 8.3, GH = 15.5) and *Erpobdella*
351 *octoculata* (Linnaeus) (AB = 1.5, GB = 3.0, GH = 8.1), were generally abundant or recorded

352 regularly being within the 'core' group; however, abundance was lowest at Abbey Bridge,
353 then higher at Garage Bend and higher still at Gasholder.

354

355 **Discussion**

356

357 The macro-invertebrate community downstream of Ironbridge 'A' power station showed a
358 varied response to the higher water temperatures. There was evidence of higher
359 invertebrate abundance at the control site, Abbey Bridge, in comparison to the site closest
360 to the thermal discharge (Garage Bend). This reduction in abundance was evident in all the
361 metrics used (total abundance, and abundance of core, occasional and EPT taxa); however,
362 samples taken at Gasholder (2 km downstream of the outfall) were generally similar to
363 samples from the control site in terms of the metrics considered. Due to the lack of
364 replicated sites it is difficult to separate changes in the community metrics in relation to
365 increased water temperature as opposed to river habitat variability. However, two potential
366 mechanisms may explain the observed patterns in abundance. Firstly, slight differences in
367 the physical structure of the river at the different sampling site may produce different
368 assemblages. For example, the Garage Bend site was slightly deeper and less turbulent than
369 the other sampling locations, while the presence of brick and tile debris at Gasholder (see
370 Table 1; Langford, 1971), may have altered community composition. Secondly, water
371 temperatures measured on the day of sampling may not adequately capture the impact of
372 historic changes in thermal regime. Although the water temperatures were very similar at
373 Gasholder and Garage Bend (Fig. 2) and approximately 4.5°C higher than Abbey Bridge, the
374 maximum temperature rise at the downstream sites could be as great as 8°C (Langford,
375 1970). Further, the highest temperature recorded was measured about 150 m downstream

376 of the outfall (31.8°C; Langford, *unpublished data*). River temperature rise was also related
377 to power station operation which was reduced both in power output and number of
378 operating hours during the study compared to historic levels (Langford, 1970). It is likely
379 therefore that downstream temperatures had historically been higher and lasted for longer
380 periods, and thus some residual effect of the disturbance history (e.g., Harding et al., 1998;
381 Foster et al., 2003, for land use) may have impacted the Garage Bend site as it was closer to
382 the outfall. Differences in EPT abundance between sites contradict the findings of Langford
383 (1971) who examined Trichoptera and Plecoptera abundance in the same reach of the River
384 Severn. This disparity may be explained by differences in the timing of study, the statistical
385 approach or the combined EPT metrics used in this study.

386 Decreases in abundance would mirror findings from both field studies and
387 experimental manipulations. A 2 – 3.5°C increase in water temperature resulted in reduced
388 invertebrate densities (Hogg et al., 1995; Hogg & Williams, 1996). Hogg and Williams (1996)
389 suggest such reductions in abundance/density may be a product of increased respiration to
390 production ratios leading to reduced resource use efficiency within the stream systems.
391 Similarly, predictions for small river systems in Wales suggest that temperature increases of
392 *ca.* 1°C may result in reduction in the springtime abundance of some macro-invertebrates
393 (Durance & Ormerod, 2007). Drawing definitive parallels between the previously highlighted
394 studies and our analysis is somewhat reduced by differences in the thermal regime of the
395 study locations. For example, the spring-fed stream of the Hogg and Williams (1996) and
396 Hogg et al. (1995) studies is likely to have a less variable thermal regime and therefore may
397 be more impacted by temperature increases. Conversely, small upland streams in Wales
398 (e.g. Durance & Ormerod, 2007) may show greater natural temperature fluctuations than
399 the larger River Severn. However, the diurnal variations downstream of the power station

400 were comparable with the regime of small streams, while the unaffected reaches upstream
401 show very little diurnal temperature variation (Langford, 1970). Reduced total invertebrate
402 abundance may impact energy transfer through the food web, potentially limiting resource
403 availability for predatory species (Durance & Ormerod, 2007). Differences in abundance
404 should be viewed with caution because of the use of hand net kick and sweep sampling
405 which can be variable whether timed or areal sampling is used (Frost et al., 1971; Furse et
406 al., 1981).

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

423 2011; Conti et al., 2014) or from specific taxonomic groups (e.g., Plecoptera) (Haidekker &
424 Hering, 2008), may respond in a similar manner.

425 Despite the thermal impact, taxonomic richness overall and for the ‘core’ group was
426 similar across sites. Conversely, ‘occasional’ and EPT taxa richness was reduced at the
427 thermally impacted Garage Bend site. The occasional group also contained a number of taxa
428 that could be described as rare transients, with only a few or even single individuals
429 recorded on a very few occasions (e.g., *Brachycercus harrisella*, Curtis, and *Ecdyonurus*
430 *dispar*, Curtis). The absence of a response from taxa within these groups at the Gasholder
431 site (which was also subject to similarly elevated temperatures) is, as with the abundance
432 metrics, likely related to either habitat variation, lack of resolution on the temperature
433 monitoring, or legacy effects of historic power station operation. Changes in taxa richness
434 have been noted in other communities associated with thermal discharges, although the
435 magnitude of the temperature increase was often greater (e.g., Poff & Matthews, 1986;
436 Langford, 1990; Wellborn & Robinson, 1996). In other studies, reduced diversity may have
437 been more related to chlorine use for anti-fouling than effects of temperature (see Langford
438 1990). However, in this study, because of the distance downstream from the outfall, the
439 very small amounts of chlorine used at the Ironbridge ‘A’ power station (target 0.02 mgL⁻¹ at
440 the outfall) chlorine decay was complete at Garage Bend and Gasholder. The trajectory
441 (increase or decrease) of temperature-mediated changes in taxonomic richness will depend
442 on the species’ physiological tolerances (Woodward et al., 2010). In field simulations,
443 taxonomic richness remained constant with water temperature increases of 3.5 – 6.5°C
444 (Hogg & Williams, 1996; Tixier et al., 2009). Bioclimatic envelope models also predict that
445 suitable climatic conditions will still persist for the vast majority of European stream macro-
446 invertebrates in the year 2080 (Domisch et al., 2013).

447 While diversity, richness and abundance provide useful overall metrics, they fail to
448 recognize changes in assemblage taxonomic composition. For example, richness may remain
449 static in relation to disturbance despite a shift in community composition from specialist to
450 generalist species (e.g., Freeman & Marcinek, 2006; Hering et al., 2009). To address this
451 issue, indicator species analysis was used to highlight taxa that showed an association with a
452 particular site or group of sites. Four taxa were significantly associated with the Abbey
453 Bridge site, *M. lacustre*, *S. reptans*, Orthocladiinae species B and *L. moselyi*. Orthocladiinae
454 species B was the only taxon present at this site and was both recorded reasonably regularly
455 and in high abundance. Orthocladiinae have been described as cold-stenothermal (Hoang et
456 al., 2006), with abundance of certain subfamilies reduced by temperature rises in
457 experimental manipulations (Nordlie & Arthur, 1981). Unlike the present study, density of
458 the blackfly larvae *S. reptans* was not significantly related to temperature in the Nemunas
459 River, Lithuania (Bernotiene, in press). Climate warming and an extreme heatwave reduced
460 richness and abundance of mollusc communities in the Saône River, France; however *M.*
461 *lacustre* was more resilient to these changes (Mouthon & Daufresne, 2006). In contrast to
462 the findings of this study, this species is thought to tolerate high summer temperatures and
463 may become the dominant sphaeriid species in response to climate warming (Mouthon,
464 2004). The fourth indicator species, *L. moselyi*, has been shown to have low egg hatching
465 success at temperatures around 20°C (Elliott, 1987), which may explain its association with
466 the colder water site in the present study. However, in contrast to our study, *L. moselyi* was
467 shown to be associated with warmer years in upland streams in the UK (Durance &
468 Ormerod, 2007). It should be noted that *L. moselyi* was generally recorded in low numbers
469 in our study and therefore inference should be treated with caution.

470 Three taxa, *S. personatum* (Garage Bend), *Hydroptila* spp. and *R. fasciata* (Gasholder)
471 were significantly associated with the thermally impacted sites. The association of *S.*
472 *personatum* with the site closest to the thermal discharge is surprising given that high
473 temperature has been suggested as a factor limiting its occurrence (Friberg & Jacobsen,
474 1999). In line with the greater abundances observed at Gasholder, *Hydroptila* abundance
475 was approximately doubled in an experimental channel subject to increased temperatures
476 of 10°C (Nordlie & Arthur, 1981). Distribution of *R. fasciata* was found to have little
477 relationship to water temperature in a Slovenian karst river (Hrovat & Urbanic, 2012);
478 however, low overall abundance in our study suggests the association of this species with
479 the Garage Bend site should be treated with caution.

480 Five species were significantly associated with the Garage Bend and Gasholder sites
481 combined. All five of these species were members of the core taxa grouping and were
482 therefore generally abundant and while they were regularly recorded at Abbey Bridge,
483 abundances were reduced at that site. *A. aquaticus*, a common species at the downstream
484 sites at Ironbridge, can acclimate to increased temperatures (Korhonen & Lagerspetz, 1996)
485 while also being able to regulate oxygen uptake (Rotvit & Jacobsen, 2013). In response to
486 elevated temperatures associated with power station discharges, *A. aquaticus* can also
487 exhibit a reduced life cycle length (Aston & Milner, 1980; Langford, 1990). Similarly, *E.*
488 *octocolata* were also significantly more abundant at Gasholder and Garage Bend than at
489 Abbey Bridge; *E. octocolata* are generally considered to be tolerant to different types of
490 anthropogenic pollution and this observation is consistent with the findings of Fey (1977)
491 who observed an increased abundance of *E. octocolata* downstream of the Elverslingen
492 power station on the River Lenne, Germany. *E. octocolata* was also common in the River
493 Trent despite the river suffering the combined effects of gross domestic sewage pollution

494 and increases in temperature due to the presence of multiple power stations (Aston &
495 Brown, 1975). *L. volckmari* was also more abundant at the warmwater sites matching a
496 study in small and medium-sized streams in Germany which found this species was
497 positively correlated with summer mean temperature (Haidekker & Hering, 2008). *B.*
498 *tentaculata* was present in greater numbers at Gasholder and Garage Bend than Abbey
499 Bridge; this may be linked to the species' ability to undertake metabolic depression to
500 acclimate to or survive unfavourable conditions (Hahn, 2005). In streams in eastern Turkey
501 abundance of *B. tentaculata* was also positively related to temperature (Sahin, 2012).

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

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

532

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534

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538

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794

795 **Tables**

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

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	✓	–		$\chi^2 = 13.21$, 1 d.f.,	$\chi^2 = 30.21$, 2 d.f.,	$z = -5.06$, $z = -4.43$	$z = 0.62$,

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

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

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

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

803

804 **Table 2** Results from indicator species analysis showing the taxa significantly associated with the three individual sampling sites and the
 805 combination of Gasholder and Garage Bend. The two components of the indicator species analysis are shown: positive
 806 predictive value (A) and sensitivity of the species (B). The results of the indicator species analysis in relation to published literature are shown;
 807 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)
<u>Abbey Bridge</u>						
<i>Musculium lacustre</i>	0.69	0.54	0.61	0.001	NS	Mouthon, 2004
<i>Simulium reptans</i>	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
<i>Leuctra moselyi</i>	0.84	0.11	0.30	0.010	No/Yes	Elliott, 1987; Durance & Ormerod, 2007
<u>Garage Bend</u>						
<i>Sericostoma personatum</i>	0.97	0.11	0.32	0.005	No	Friberg & Jacobsen, 1999
<u>Gasholder</u>						
Hydroptila spp.	0.79	0.35	0.53	0.005	Yes	Nordlie & Arthur, 1981
<i>Rhyacophila fasciata</i>	0.80	0.18	0.38	0.002	NS	Hrovat & Urbanic, 2012

Gasholder and Garage Bend

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

808

809 **Figure captions**

810

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

813

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

819

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

823