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1 **Persistence in the longitudinal distribution of lotic insects in a changing**  
2 **climate: a tale of two rivers**

3

4 Running head: Persistent longitudinal distribution of lotic insects

5

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29 Key words : river temperature, caddisflies, Trichoptera, environmental

30 change, net-spinners, Hydropsychidae, spatial mismatch

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33

34

35 **Abstract**

36

37 The longitudinal distribution of many taxa in rivers is influenced by  
38 temperature, and we postulated that a past increase in river temperature  
39 should have resulted in cool-adapted species retreating further into the  
40 headwaters and warm adapted species expanding upstream. Using data on  
41 net-spinning caddisflies (Hydropsychidae), we repeated earlier surveys of the  
42 longitudinal distribution of species along the Welsh Usk and the French Loire,  
43 and assessed changes in species occurrence and relative abundance at the  
44 resampled sites, matched with information on water temperature over the  
45 same periods. Distributional changes in the Usk were slight between 1968/69  
46 and 2010, one rare species appearing at a single headwater site and one  
47 warm-adapted species disappearing from the main river, with no significant  
48 changes in the longitudinal distribution of the species. Distributional changes  
49 in the Loire, between 1989-93 and 2005, were similarly modest, with no  
50 consistent movement of species up- or downstream. The mean decadal rate  
51 of temperature increase in the Usk was a modest 0.1 °C in a 'summer cool'  
52 headwater site, while a 'summer warm' tributary increased by 0.16°C per  
53 decade, and the main river by 0.22°C. The Loire is warmer than the Usk and  
54 the mean decadal rates of increase, over the period 1989-2005, at three sites  
55 along the lower reaches were 0.39, 0.48 and 0.77 °C. Increases in stream  
56 and river temperature were spatially variable, therefore, and not associated  
57 with consistent upstream movement of species. We conclude that either the  
58 temperature increases have hitherto been insufficient to affect species  
59 distribution or, of more potential concern, that it may not be possible for river  
60 organisms (that do not respond only to temperature) to move because of a  
61 developing spatial mismatch between key habitat characteristics, some of  
62 them changing with the climate but others not.

63

64

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68

69 **Introduction**

70

71 Temperature is often regarded as a 'master factor' in ecology, affecting  
72 almost all aspects of life at a range of levels of organisation from individuals to  
73 networks (Brown *et al.*, 2004; Yvon-Durocher, 2010). Rising global and  
74 regional temperature, therefore (observed already and predicted for the future  
75 due to anthropogenic effects), should be accompanied by ecological changes  
76 that can be expected to accelerate (IPCC, 2014). Ecology has a long history  
77 of studies relating shifts in the phenology and range of species to previous  
78 fluctuations in the climate, and there is a great deal of evidence for such  
79 ecological responses in a wide range of terrestrial, marine and freshwater  
80 systems (e.g. Parmesan, 2006). Temperature has long attracted a great deal  
81 of attention in freshwater systems (Macan, 1963; Elliott, 1994), and its  
82 importance and mode of action was studied by physiological ecologists  
83 substantially before more recent widespread concerns about anthropogenic  
84 global climate change (e.g. Burton & Odum, 1945; McLeese, 1956; Pleskot,  
85 1961; Parmesan, 2006).

86

87 Shifts in distribution are among the most obvious effects of the  
88 changing climate and have been widely reported, usually in the context of  
89 poleward shifts in range or movements upslope on mountains (e.g. Parmesan  
90 *et al.*, 1999; Chen *et al.*, 2011; Feary *et al.*, 2014). In the particular context of  
91 river systems, longitudinal (and therefore altitudinal) patterns in distribution, in  
92 which species are represented sequentially along the channel, are almost  
93 universal (Illies & Botosanenu, 1963; Hynes, 1970; Statzner & Borchardt,  
94 1994). Many such patterns have been ascribed to differences in temperature  
95 along the river, where the water is essentially warmer in downstream reaches  
96 (Ward, 1992).

97

98 Apparent 'radiations' of related species, occupying habitats with  
99 different thermal regimes, have been described in a number of groups (e.g.  
100 Ide, 1935; Macan, 1961, 1963; Vannote & Sweeney, 1980). In some cases,  
101 there is evidence of physiological adaptations to temperature, which are  
102 thought to underlie the observed longitudinal distribution. A prominent

103 example is a globally-distributed family of net-spinning caddis flies, the  
104 Hydropsychidae, whose abundant larvae are important 'ecosystem engineers'  
105 and suspension feeders in rivers and streams, increasing the retention  
106 nutrients and carbon within the river ecosystem (e.g. Wallace, Webster &  
107 Woodall, 1977; Albertson & Daniels, 2016). A number of researchers  
108 independently found that the respiratory physiology of various species in this  
109 family appears to match the thermal environment. Thus, Hildrew & Edington  
110 (1979) showed that *Diplectrona felix* is a species of extreme headwaters,  
111 being replaced downstream first by *Hydropsyche instabilis* and then by  
112 *Hydropsyche siltalai* and *Hydropsyche pellucidula* and others. This spatial  
113 pattern in one Welsh river was correlated with increasingly warm summer  
114 conditions, *D. felix* never occurring where the daily maximum in summer  
115 exceeded 15 °C (i.e. they were restricted to 'summer cool' streams). They  
116 also showed (Edington & Hildrew, 1973; Hildrew & Edington, 1979) that, in  
117 three of these species, resting metabolic rate was relatively independent of  
118 temperature under conditions that matched those of the respective river  
119 reaches occupied, and which they suggested maximised growth efficiency in  
120 nature. Similarly, Lowe & Hauer (1999) related the longitudinal distribution of  
121 two species of hydropsychids in the northern Rocky Mountains to river  
122 temperature, and again found that differences in the metabolic rate-  
123 temperature relationship were consistent with their longitudinal distribution.  
124 Further, Roux *et al.* (1992) showed that the 'amplitude' of metabolic rate over  
125 the range of environmental temperatures from 5 to 25 °C increased with  
126 stream order (increasing stream size) in five European species of  
127 *Hydropsyche* in the River Rhône. There is thus considerable circumstantial  
128 and experimental evidence of a key role for temperature in the longitudinal  
129 distribution of this group of insects, and therefore grounds to expect that the  
130 distribution might change with consistent warming.

131

132 River temperatures are widely, though not universally, thought already  
133 to have increased over the last decades. For instance, Kaushal *et al.* (2010)  
134 found that 20 out of 40 major streams and rivers in the continental United  
135 States had warmed over various periods, some up to 100 years, though the  
136 warming trend was strongest at urbanised sites. Further, Orr *et al.* (2015)

137 collated spot temperature data for 2773 sites in England and Wales between  
138 1990 and 2006 and found a warming trend for 86% of them, most by less than  
139 1 °C in terms of mean annual temperature, while Durance & Ormerod (2007)  
140 estimated that some streams in mid-Wales had warmed by 1.4 °C (forested)  
141 and 1.7 °C (moorland) between 1981 and 2005. However, Arismendi *et al.*  
142 (2012) examined records from 63 stream sites in the Pacific continental  
143 United States and found mostly warming trends where records began in the  
144 1950s but most streams had apparently cooled or had not changed at sites  
145 where records began in the late 1980s. They concluded that ‘our perspective  
146 of climate impacts on stream temperature is clouded considerable by a lack of  
147 long-term data on minimally impacted streams’. While river temperature is  
148 primarily driven by air temperature (Caissie, 2006), there is a large amount of  
149 spatial and temporal heterogeneity, which is a challenge to prediction (Webb  
150 *et al.*, 2008), particularly because the uplands are under-represented in  
151 records. Indeed, in England and Wales, only six sites of those assessed by  
152 Orr *et al.* (2015) were over 300m in altitude.

153

154         Some ecological changes in streams and rivers have been attributed to  
155 rising temperature. For instance, southern, thermophilic species of fish and  
156 invertebrates replaced cool water species in the Upper Rhone River in  
157 France, consistent with a warming of the river of about 1.5 °C between the  
158 late 70s and the late 90s (Daufresne *et al.*, 2003), while the abundance of  
159 many invertebrate taxa in circumneutral, upland Welsh streams declined  
160 between 1981 and 2005, apparently in response to warming (Durance &  
161 Ormerod, 2007). Further, Sheldon (2012) repeated a survey of two species of  
162 stoneflies in the Great Smoky Mountains National Park after almost 30 years  
163 (1977/78 to 2006) and found that one had moved uphill by 60-250m,  
164 apparently consistent with warming, although the other had not. Such re-  
165 examination of detailed past records of distribution can be thus particularly  
166 useful in detecting distributional changes that have actually been measured  
167 rather than inferred or predicted.

168

169         Opportunities to replicate previous studies after significant periods of  
170 time are relatively few and here we took advantage of earlier ‘snapshot’

171 surveys of the longitudinal distribution of hydropsychid larvae from two  
172 contrasting river systems, the Welsh Usk (assessed in 1968-1970; Hildrew &  
173 Edington, 1979) and the French Loire (assessed from 1989-1993; Ivol *et al.*,  
174 1997). While the rivers are very different, the clear, and rather similar,  
175 distribution of hydropsychid larvae along both systems is an example of the  
176 classical sequential replacement of species in rivers (Hildrew & Edington,  
177 1979; Statzner & Dolèdec, 2011), with which temperature (among other  
178 physical factors) has been implicated. We expected that water temperature  
179 would have increased in both systems and postulated that the distribution of  
180 species would have changed, as warm-adapted species from downstream  
181 moved further upstream and cool adapted species in headwaters retreated up  
182 the slope.

183

## 184 **Methods**

185

### 186 *Site description*

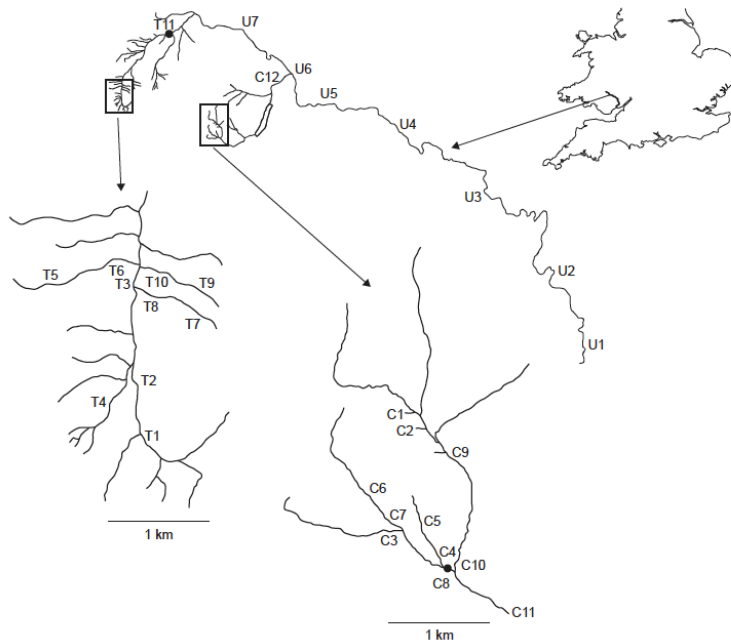
187

188 The Usk is a small river by world or European standards (catchment  
189 area 1358 km<sup>2</sup>; length 120 km), though one of the largest in Wales. It rises at  
190 above 500m and flows east and south to join the Severn Estuary near the  
191 town of Newport. It has a predominantly upland and rural catchment with a  
192 fairly sparse population density (<20 people km<sup>2</sup>), and drains sandstones and  
193 mudstones of the Old Red Sandstone Series. It is designated a 'Special area  
194 of Conservation' and is an important salmonid fishery. Most of the main river  
195 and headwaters are in good or moderate ecological status (Environment  
196 Agency, 2009). Mean annual nitrate concentration in much of the catchment is  
197 mainly below 1 mg L<sup>-1</sup> and phosphate below 0.03 mg L<sup>-1</sup> (Larson & Ormerod,  
198 2009).

199

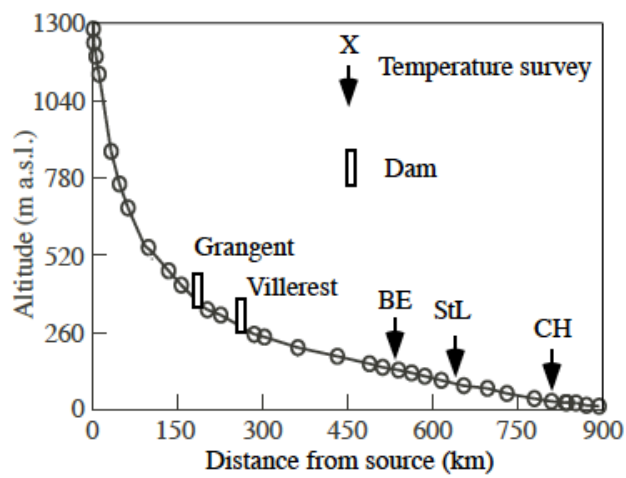
200 Sampling focussed on the main river and on two important south-bank  
201 headwaters (the Afon Tarell and the Caerfanell systems) of the Usk, draining  
202 the northern flanks and/or north-eastern flanks of the Brecon Beacons (a  
203 National Park in south Wales), with upland catchments of rough grazing with  
204 some semi-native woodland and coniferous forestry (Fig. 1a). These are

205 typical upland stony/rocky streams with fast flowing water and channel widths  
 206 up to about 4.5 m. Discharge, though permanent, is flashy and responds  
 207 quickly to rainfall.  
 208



209  
 210

a)



211

b)



212 **Fig. 1** Map of (a) the River Usk and sampling sites (inset showing location in  
213 England & Wales), plus details of the two south-bank tributaries; the Afon Tarell to  
214 the west and the Caerfanell to the west (for site codes see Table 1: note that the  
215 normal limit of tidal influence on the wholly freshwater course of the Usk is about 1km  
216 downstream from site U1); and b) longitudinal profile of the Loire showing sampling  
217 sites (open circles), position of large dams and of sites with information about  
218 temperature at Belleville-sur-Loire (BE), Saint-Laurent-des-Eaux (StL) and Chinon  
219 (CH).

220

221 The environmental status of the Loire has been synthesized several  
222 times (e.g. Billen *et al.*, 1995; Rodrigues, 2004; Oudin *et al.*, 2009 and see  
223 text, and many thematic maps on environmental catchment characteristics  
224 available at <http://info-sed.plan-loire.fr/fiche-document/?iddocs=12>). By  
225 comparison with the Usk, the Loire is an extremely large river, with a  
226 catchment area of 117 054 km<sup>2</sup> and a course of over 1000 km, rising in the  
227 Massif Central at 1408 m. It drains 20% of mainland France. As such, it is  
228 much more diverse than the Usk geographically, geomorphologically and  
229 geochemically. There are acidic, siliceous rocks in the Massif Central,  
230 contrasting with calcareous areas in the middle Loire, and zones of granitic  
231 bedrock. Much of the catchment is heavily agricultural, with urban  
232 development and some industry. Quite polluted over much of the length of the  
233 main river in the nineteenth century, improvements in water treatment have  
234 reduced phosphorus and nitrate concentration and in phytoplankton in the  
235 water column since about 1980 (Oudin *et al.*, 2009). Overall, water quality has  
236 been improving over that period and the river is now in good to moderate  
237 ecological condition for much of its length. Much of the Loire still has natural  
238 flow dynamics, especially because the fluvial morphology is still relatively  
239 natural. However, there are numerous sills and barrages throughout the  
240 catchment that affect the discharge and temperature dynamics. For example,  
241 on average 7 m<sup>3</sup> s<sup>-1</sup> of water is now diverted from the upper Loire catchment  
242 into the [Ardèche](#) catchment (Valentin, 1995). Greater effects are caused by  
243 the biggest reservoir on the river at Villerest (Fig. 1b) that limits flood peaks to  
244 1000 m<sup>3</sup> s<sup>-1</sup>, sustains minimum flow all year at around 8 – 10 m<sup>3</sup> s<sup>-1</sup> just below  
245 the dam and at 60 m<sup>3</sup> s<sup>-1</sup> near the first nuclear power plant on the river at

246 Belleville (Fig. 1b) (Oudin *et al.*, 2009), and releases cold hypolimnic water.  
247 Biological sampling in the Loire [focussed](#) on the distribution patterns along a  
248 large river, and the arrangement of sites therefore differed from that on the  
249 Usk, as they were all on the main river (Fig. 1b) and tributaries were not  
250 included.

251

### 252 *Species Distribution*

253

254 Older data were available from 11 sites in the Caerfanell sub-  
255 catchment (sites C1-11) and 11 sites (sites T1-11) on the Afon Tarell (Fig. 1a)  
256 from April 1968 (Hildrew & Edington, 1979), and from seven on the main river  
257 (U1-7) and three in the Caerfanell system (C4, C11 and C12) in late  
258 April/early May 1970 (Fig. 1a). Thus, two sites in the Caerfanell system (Sites  
259 C4 and C11 in Fig. 1a) were sampled in both campaigns (1968 and 1970),  
260 yielding a total number of sites from the Usk system of 30. All 30 were  
261 resampled in April 2012. The methods used were identical in both cases  
262 (apart from the advancing decrepitude of the sampler), consisting of turning  
263 and scrubbing stones just upstream of a hand net (250 µm mesh) for a timed  
264 period. This was done in riffles for a minimum of five minutes in the earlier  
265 surveys, and for exactly five minutes in the later surveys. All data are  
266 expressed per 5-minute search. Thus, these semi-quantitative data are  
267 comparable between the two campaigns.

268

269 There have been a number of surveys of hydropsychids in the Loire.  
270 Ivol *et al.* (1997) report collections from 38 sites in 1989, 1991 and 1993,  
271 while Statzner *et al.* (2010) and Statzner & Dolèdec (2011) sampled most of  
272 the same sites in 2005. We collate here data from 32 sites with accessible  
273 hydropsychid habitat on the Loire sampled by both teams (Fig. 1b) ranging  
274 from 1 to 893 km from the source in the Massif Central and over an altitudinal  
275 gradient of over 1200m. The sites are arranged in a simple longitudinal  
276 sequence downstream from the source. Ivol *et al.* (1997) describe searches  
277 using a hand-net (mesh 0.5mm) for 10 minutes at each site, brushing stones  
278 into a container and preserving the samples onsite and sorting and counting  
279 them in the laboratory. The later surveys were carried out by two people,

280 picking up large stones and pieces of dead wood and brushing them into a  
281 similar hand-net for 20 minutes. Samples were again sorted and counted in  
282 the laboratory. Thus, surveys on the Loire, while using basically similar  
283 methods, were carried out by different teams and with differing intensity, so  
284 we compare these data only in terms of presence/absence and relative  
285 abundance.

286

287 It is important to note that the two studies were carried out for different  
288 original purposes and with differing designs, although they sampled a similar  
289 number of sites overall. The most important contrast is that the Usk study  
290 incorporated a network of sites, concentrated in two headwaters of a short  
291 river (though also including the mainstem) and was aimed at assessing the  
292 consistency of relatively small-scale, longitudinal species sequences of  
293 species. Larvae only were counted. The Loire study was at a much larger  
294 spatial extent over a long continental river and, because it aimed at  
295 elucidating the longitudinal distribution of species (both larvae and pupae  
296 were identified and counted), used a simple downstream sequence of sites  
297 from source to mouth, ignoring the branching nature of the river. This limits  
298 the comparability of the data between studies, though it does not preclude a  
299 similar search for patterns of longitudinal/altitudinal changes in both.

300

### 301 *Water temperature*

302

#### 303 The Usk

304

305 Temperature records were available from a previous study in the  
306 Caerfanell system in 1968-1969, using early continuous temperature  
307 recorders [Grant Instruments (Development) Ltd., Cambridge, UK] (Edington  
308 & Hildrew, 1973; Hildrew & Edington, 1979). These used thermistor probes as  
309 temperature sensors, accurate to within 0.5°C as checked against a mercury-  
310 in glass thermometer before deployment. They were used at four stream sites  
311 (C3, C7, C8 and C10; Fig. 1a) from 18 July 1968 to 31 July 1969. They are  
312 first (site C3, mean channel width <1m), second (C7, C8; mean channel  
313 widths 2-3m) and third order (C10; mean channel width 4-5 m), within c 1.0

314 km of each other and at altitudes of 392, 389, 324 and 312m for sites C3, C7,  
315 C8 and C10, respectively. Sites C3, C7 and C8 have continuous riparian  
316 strips of semi-natural deciduous woodland largely backed by mature  
317 coniferous plantation forest, whereas C10 has a thin and discontinuous  
318 riparian strip of semi-native woodland backed by open moorland. A further  
319 record was obtained from the lowland reach of the River Usk at Chain Bridge  
320 (Fig. 1a, site U2; altitude 39m) from 6 October 1969 to 1 August 1970, with  
321 some breaks due to malfunction and vandalism. From these records we  
322 extracted daily maxima and minima at each site over these periods.

323

324 Contemporary records of temperature were obtained for exactly the  
325 same four headwater sites in 2012-2013, using Onset Hobo water  
326 temperature recorders (Pro v2) taking readings every 15 minutes from June  
327 2012 to September 2013. Recorders were placed in the margins of the  
328 streams and encased in drainage bricks to protect them from direct sunlight  
329 while allowing water throughput. Recorders at sites C3 and C10 were  
330 displaced by high flow events in spring 2013 and recordings beyond March  
331 were thus omitted from the analysis for those two sites. Hobo loggers have a  
332 stated accuracy of 0.2°C, and this was confirmed by testing the four loggers at  
333 0°C and 30°C before deployment in the field.

334

335 Since we had no measured data for the intervening years between the  
336 studies, we modelled monthly water temperature from monthly air  
337 temperature using sigmoid functions. Sigmoid functions are considered to be  
338 a better alternative to linear functions when using air temperature as the  
339 single independent variable to predict stream temperature (Mohensi *et al.*,  
340 1998). Indeed, while linear regression analysis is widely used to model water  
341 from air temperatures (e.g. Stefan & Preud'homme, 1993; Durance &  
342 Ormerod 2007), it is recognized that, at extreme values of air temperatures,  
343 the relationship between daily water and air temperature departs from  
344 linearity. This is because, at high temperature, non linearity arises due to  
345 evaporative cooling (Mohensi *et al.*, 2002), while at low air temperature, non-  
346 linearity arises because water temperature is buffered by hyporheic and

347 phreatic water and freezes only when air temperature drops significantly  
348 below 0°C (Crisp & Howson, 1982).

349

350         Since air temperature at the four stream sites and one river site has not  
351 been monitored (no weather station within 100km covered the period of  
352 interest, 1968-2013), we used the long-term air temperature record from the  
353 5km gridded models of UKCIP (UK's Climate Impact Programme). All four  
354 stream sites were contained within one 5km square, and we extracted daily  
355 mean and maximum air temperature data from July 1968 to September 2013  
356 from that square. We extracted similar data from the 5km square containing  
357 the River Usk site.

358

359         As air temperature fluctuates far more than water temperature due to  
360 the higher thermal mass (or heat capacity) of water, we maximized potential fit  
361 between water and air temperatures by using mean air temperature to predict  
362 minimum and maximum water temperature. For the four stream sites we  
363 created the models using the 2012-13 daily records. The models were tested  
364 on the 1968-69 daily data for validity. The modelled sigmoid functions were  
365 then used to predict maximum monthly stream temperatures from monthly air  
366 temperature for the four streams from July 1968 to September 2013. For the  
367 River Usk model, as water temperature records were available only for 1969-  
368 70, we used those data to create the model, and then used the model to  
369 predict maximum monthly river temperatures from July 1968 to September  
370 2013. Here we present primarily the modelled mean daily maximum summer  
371 temperatures (June, July, August) for the whole period, as the most  
372 meaningful ecologically. All analyses were done using Minitab 17.

373

374         The Loire

375

376         For the Loire, we used the measured and modelled data of Electricité  
377 de France (EDF) (methods, data and modelling results courtesy of Dr Alain  
378 Poirel, EDF). The entire data set covered the period from 1949 to 2013. From  
379 these, we selected the period covered by our biological data (1989-2005).  
380 Here, we used the measured or modelled mean of the daily maximum water

381 temperature for the three summer months (June, July, August) at locations  
382 upstream of three nuclear power plants distributed along the lower Loire (Fig.  
383 1b). Where available, we used measured data and complemented periods  
384 with missing values using modelled data.

385

386         For the 17 summers covered by our biological data, Belleville and St.  
387 Laurent had 16 measured values each, whereas Chinon had only five  
388 measured values. The combined accuracy of probe and transmitter of hourly  
389 measured values was 0.3°C. These hourly measured values in the longer  
390 (i.e. 1949-2013) data set served to model hourly data for summers with  
391 missing values. In the past, EDF and the Université of Tours co-operated to  
392 improve predictions of river temperature from measured air temperature and  
393 river discharge (e.g. Moatar & Gailhard 2006; Bustillo et al. 2014). In our case,  
394 the predictions were obtained using neural network models with one hidden  
395 layer of four neurons fixed on half of the samples and tested on the other half  
396 per site, including the variables: a) mean daily air temperature, b) mean daily  
397 discharge, and c) day and night length, and applying root-mean-square-error  
398 scaling. These analyses indicated that the model precision varied from about  
399 0.8°C (Chinon) to about 1°C (Belleville). Given that Chinon had fewer  
400 measured values than the other two sites, the apparently better model  
401 precision did not indicate more reliable overall temperature patterns over our  
402 17 years.

403

## 404 **Results**

405

### 406 *Distribution*

407

408         Five hydropsychid species were found on the Usk in both surveys, one  
409 species of *Diplectrona*, one of *Cheumatopsyche* and three in *Hydropsyche*,  
410 whereas one further species of *Hydropsyche* occurred only in the original  
411 survey and another only in the recent survey (Table 1a). In the Loire, eight  
412 species were taken in both surveys, seven species in *Hydropsyche* and one in  
413 *Cheumatopsyche*, while two further *Hydropsyche* species appeared in the  
414 more recent data only (Table 1b). Both studies included a substantial fraction

415 of the hydropsychid fauna of both regions and all species known from both  
416 rivers were found in one or both surveys. The 'densities' (as numbers caught)  
417 differed between occasions in both the UK and French studies. In the Loire,  
418 more individuals were taken in the more recent survey for all species except  
419 *H. bulgaromanorum* (Table S1 in Supporting Information), which no doubt is  
420 largely accounted for by the greater sampling effort in the latter, so we could  
421 not test statistically for density differences in the two studies. In the Usk,  
422 where estimates were more comparable (see Methods), densities were not  
423 significantly different between the two studies, except those of *H. siltalai* in the  
424 Caerfanell and the main river, in both of which the species was less abundant  
425 in 2012 than in 1968/70 (Table S1).

426

427 In terms of simple presence and absence, there were remarkably few  
428 changes in species complement in the Usk system between 1968/70 and  
429 2012 (Table 1a). With one exception, all species present in the earlier  
430 samples were also taken at the same sites in 2012. The species most typical  
431 of larger rivers, *Hydropsyche contubernalis*, was not taken in the more recent  
432 survey (and further searches have consistently failed to find it in recent years).  
433 One new headwater species appeared, however, the rare *Hydropsyche*  
434 *fulvipes* being taken at one small stream on the Afon Tarell system at about  
435 800 m from the source and at an altitude of 417 m. It has not been taken  
436 previously in the Usk or its tributaries, but is present at a very few similar sites  
437 elsewhere in South Wales. Overall, there was no evidence of an upstream  
438 shift in hydropsychid species in the Usk over the 45 years between samplings.  
439 There were rather greater differences in the species occurrence detected in  
440 samples from the Loire (Table 1b). *Hydropsyche instabilis* and *H.*  
441 *angustipennis* were taken only in the more recent sampling, while  
442 *Hydropsyche siltalai* and *H. ornatula* had a wider distribution latterly. All other  
443 species had a similar longitudinal occurrence in the two surveys, with no  
444 consistent evidence for an upstream shift in their ranges.

445

Table 1. Species presence (+) or absence (-) in the River Usk (a) and the Loire (b). Sites ordered by descending altitude (for site numbers and locations see Fig. 1). At each intersection in the table the first/second symbol indicates presence (+)/absence (-) in the early/recent data, respectively (blanks indicate the species was found on neither occasion). River Usk early data 1968/1970, recent 2012; River Loire early data 1989/1991/1993, recent 2005 (see text for details).

(a)

Site	Alt (m)	Source distance (km)	<i>D. fel</i>	<i>H. fulv</i>	<i>H. inst</i>	<i>H. silt</i>	<i>H. pell</i>	<i>H. cont</i>	<i>Ch. lep</i>
C1	513	0.2	++						
C2	469	<0.1	++						
C9	455	0.5			++	++			
C5	436	0.2	++						
C6	419	1.7	-+		++				
T5	417	0.8	++	-+					
C7	392	2.0	-+		++	+-			
C3	389	0.5	++		++				
T7	372	0.2	++						
T9	367	0.4	++						
T1	360	3.9			++	+-			
T4	344	3.0			++	+-			
C4*	336	0.6	++						
T6	329	1.5	++		+-				
C8	324	2.3	+-		++	+-			
T2	321	4.5	-+		++	++			
C10	312	3.5			++	++			
T8	308	1.0	++		++				
T10	301	1.0	++		++				
T3	288	5.4			++	+-			
C11*	276	4.1			++	+-			
T11	171	12.3			++	++			
C12*	152	13.7				++	++		
U7	131	21.2				++	++		
U6	117	27.3				++	++		
U5	99	33.6				++	++		
U4	68	41.3				++	++		
U3	45	56.7				++	++		
U2	39	68.4				++	++	+-	
U1	16	77.2				++	++	+-	++

\* these sites were sampled in both the 1968 and 1970 surveys, and had the same species complement.



(b)

Site	Alt (m)	Source distance (km)	<i>H. inst</i>	<i>H. din</i>	<i>H. silt</i>	<i>H. incog</i>	<i>Ch. lep</i>	<i>H. cont</i>	<i>H. exo</i>	<i>H. ang</i>	<i>H. orn</i>	<i>H. bulg</i>
2	1282	1.0	- +	++	+ -	+ -						
3	1236	2.0	- +	++	++							
4	1190	5.8	- +	+ -	++							
5	1130	11.1		+ -	++	- +						
6	870	32.3			++	++						
7	760	47.2			- +	++	- +					
8	680	62.2			- +	++	- +					
9	532	104.6			- +	++	++	++	++			
10	468	133.9				++	++	++	++			
11	420	156.2				++	++	++	++			
13	337	202.3				++		++	- +	- +		
14	319	225.9				++	- +	++	++			
16	254	284.9				++	++	++	- +	- +		
17	245	302.9				++	++	++	- +			
18	209	362.1				+ -	++	++	++			
19	180	431.7					- +	++	++		- +	
20	155	488.4					- +	++	++		- +	
21	143	511.7					+ -	++	++		++	
22	134	539.8					- +	++	++		- +	
23	124	562.7					- +	++	++		- +	
24	113	586.1					- +	++	++		- +	+ -
25	99	615.2					- +	++	++		- +	
26	81	654.8					+ -	++	++			
27	72	696.4					++	++	++			
28	55	730.9					- +	++	++			- +
29	37	779.3					++	++	++			
30	28	809.6					- +	++	++			- +
31	24	834.1					++	++	++			++
32	23	836.9					- +	++	++			++
34	23	852.7					- +	++	++			++
37	15	871.2						++	++			++
38	12	893.4						++	++			++

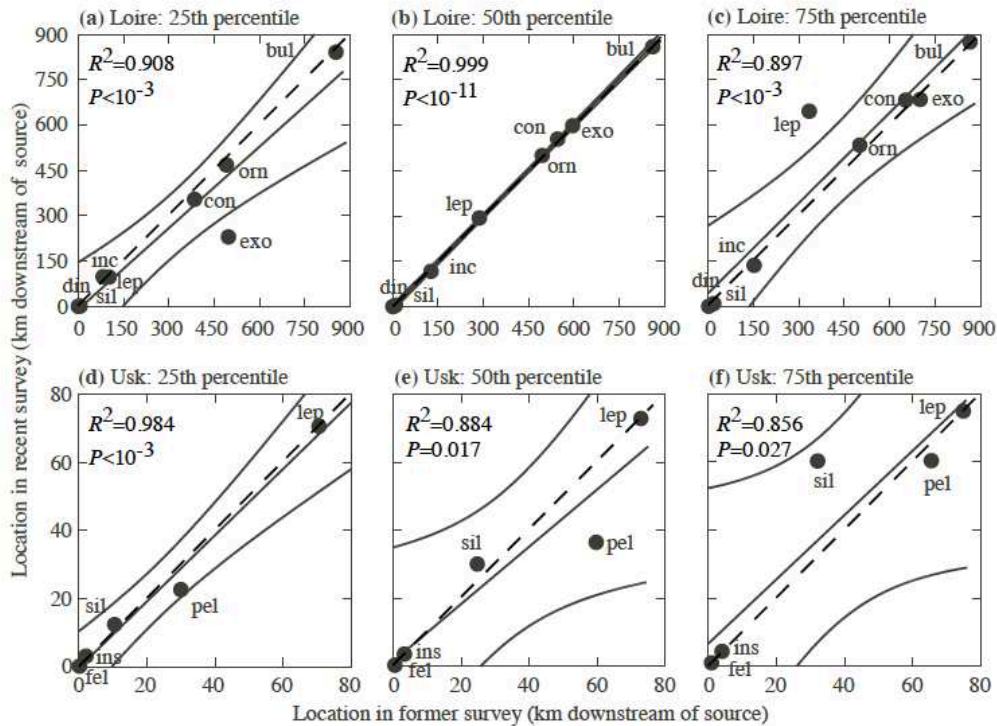
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448

449

450 In terms of the longitudinal distribution of relative abundances of the  
451 species (Fig. 2), in the Loire, the regression of the 50<sup>th</sup> percentile of the recent  
452 distribution of species on their former distribution shows that all species fall  
453 close to the x=y line (where there is no change) (Fig. 2b). The 25<sup>th</sup> percentile

454 regression shows *Hydropsyche exocellata* falls outside the 95% CL, and that  
 455 it was relatively more abundant upstream in the recent data, though there was  
 456 no overall extension of its range (Table 1b) or any change in the position of its  
 457 50<sup>th</sup> or 75<sup>th</sup> percentile distribution. Thus, it was not found at sites 13, 16 and



458  
 459 **Fig. 2** Plots of the 25<sup>th</sup>, 50<sup>th</sup> and 75% percentiles of the cumulative relative  
 460 abundance of hydropsychid species in (a,b,c, respectively) the Loire and (d,e,f,  
 461 respectively) the Usk, comparing the 'old' (x) and 'new' (y) data. Points show the  
 462 position (km downstream) at which 25, 50 or 75% of the final total numbers of that  
 463 species had been collected, moving downstream. Lines are  $x=y$  (broken) plus linear  
 464 regression and upper and lower 95% CL of the regression. Species abbreviations:  
 465 bul – *Hydropsyche bulgaromanorum*, con - *H. contubernalis*, din – *H. dinarica*, exo –  
 466 *H. exocellata*, fel – *Diplectrona felix*, inc - *H. incognita*, ins – *H. instabilis*, lep –  
 467 *Cheumatopsyche lepida*, orn – *H. ornatula*, pel – *H. pellucidula*, sil - *H. siltalai*.

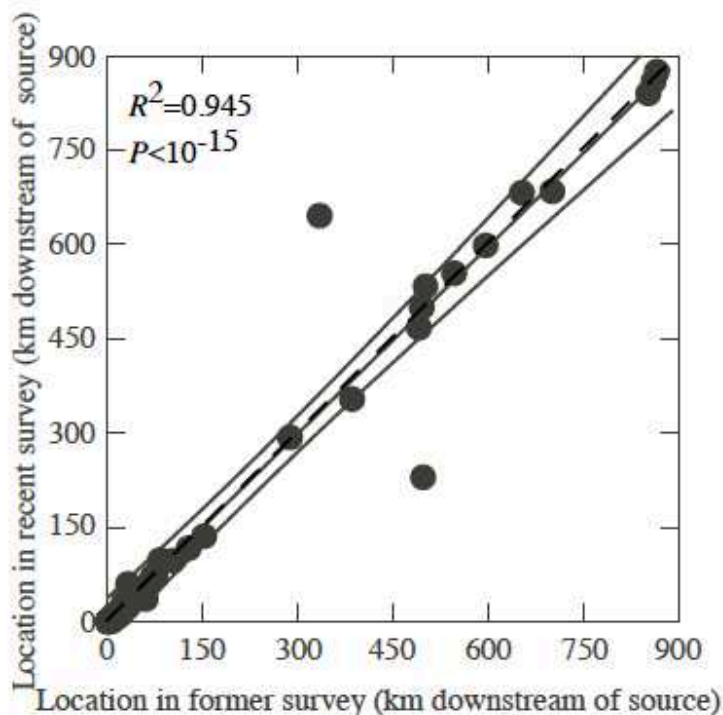
468  
 469  
 470 17 in the previous data set (Table 1b). Conversely, the 75<sup>th</sup> percentile of the  
 471 distribution of abundance of *Cheumatopsyche lepida* was further downstream  
 472 in the recent data, consistent with its more widespread occurrence at sites in

473 the lower reaches of the river (Table 1b). In the Usk, the points for all five  
474 hydropsychid species fall within the equivalent 95% confidence intervals for all  
475 three regressions (though these are rather wide; Fig. 2d, e and f), consistent  
476 with the very similar distribution of all species at all sites in terms of  
477 presence/absence.

478

479 Plotting together all species from both rivers, and data from all three  
480 percentiles of the relative cumulative downstream abundance, in both the  
481 recent and older datasets, shows that all species fall close to the line  $x=y$ ,  
482 save only the points for the 25<sup>th</sup> percentile of *H. exocellata* and the 75<sup>th</sup>  
483 percentile of *C. lepida*, both in the Loire (Fig. 3). There is thus no sign of any  
484 overall or consistent shift of species up- or downstream in these two rivers.

485



486

487 **Fig. 3** Points for the 25<sup>th</sup>, 50<sup>th</sup> and 75<sup>th</sup> percentiles of the cumulative relative  
488 abundance of all species in both rivers from Fig. 2 analysed in one regression (see

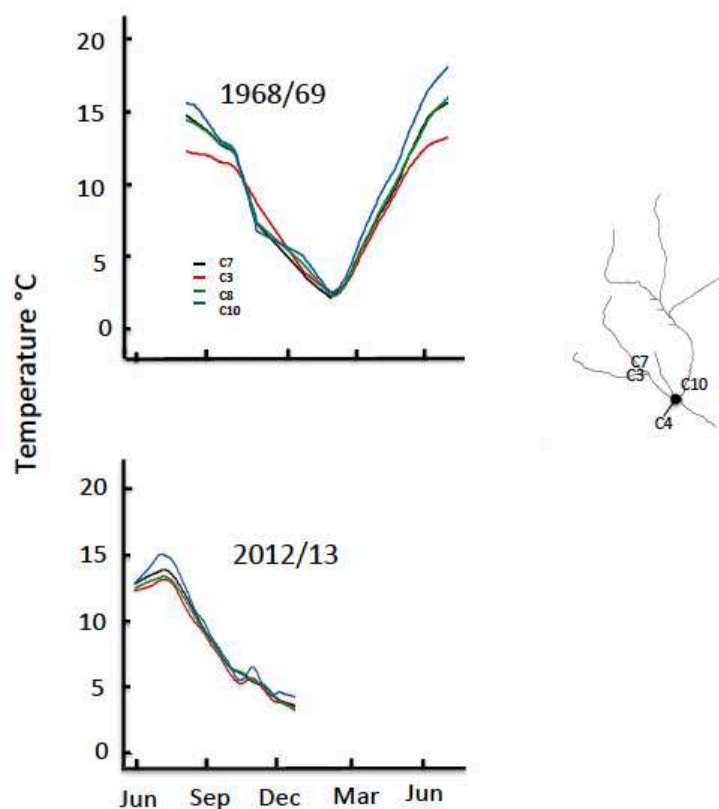
489 Fig. 2 for further details). The two outliers are *Cheumatopsyche lepida* (25<sup>th</sup>  
490 percentile in the Loire, point above the line) and *Hydropsyche exocellata* (75<sup>th</sup>  
491 percentile in the Loire, point below the line).

492

### 493 *Temperature*

494

495 We have annual records of daily stream maxima/minima for four sites in  
496 the Caerfanell sub-catchment in the Usk for the whole of in 1968/69 and the  
497 first half of 2012/13 (equipment failed in the latter half of the year at two sites).  
498 From smoothed (Lowess) curves of daily maxima, it is clear that the  
499 relationship among the sites was consistent between the two years, C10  
500 being warmest in summer and C3 the coolest (Fig. 4). The daily maximum  
501 temperature attained at these two sites differed by as much 4°C in summer,  
502 and this was true in both the older and more recent data, while the daily range  
503 in the warmer stream was also much greater (daily range  $\pm$ sd of  $3.46 \pm 0.51$  in  
504 the warmer stream, C10, versus a daily range of  $1.26 \pm 0.08$  in the cooler  
505 stream, C3).



506

507 **Fig. 4** Smoothed (Lowess) plots of measured daily maximum stream temperature at  
508 four sites in the Caerfanel sub-catchment of the Usk (inset, C7, C3, C8 and C10; Fig.  
509 1a) in 1968/69 and for the first half of 2012/13.

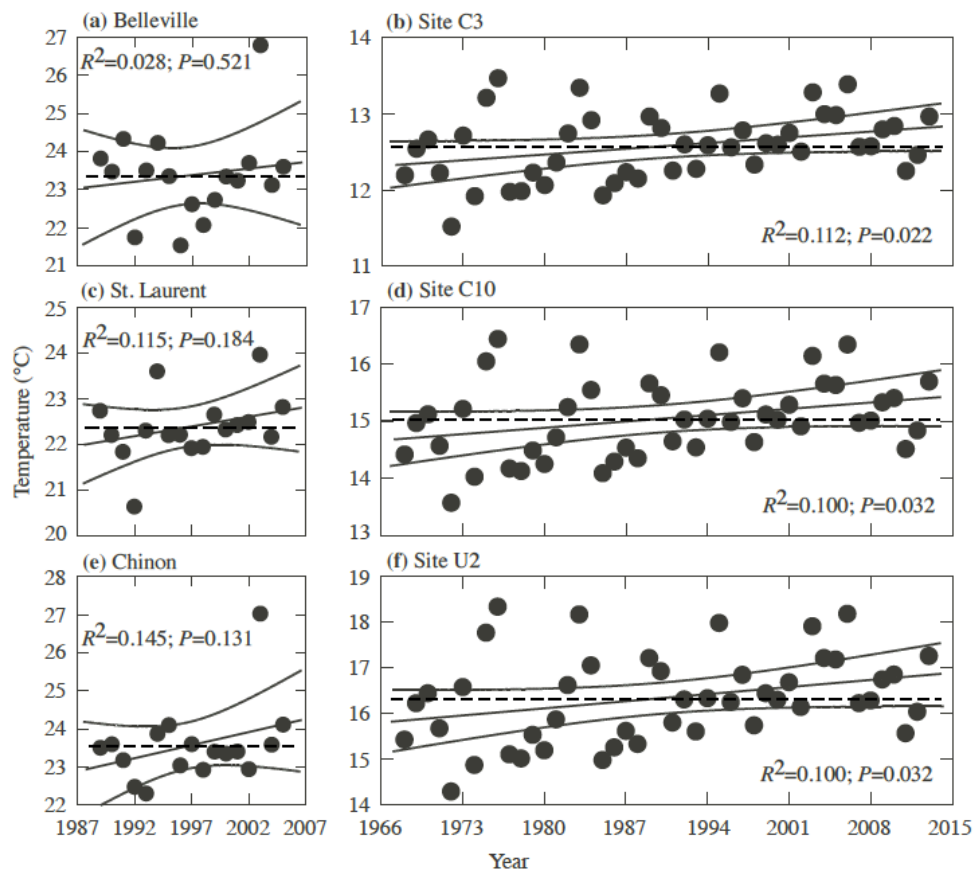
510

511 We modelled the mean daily maximum stream temperature attained in  
512 summer (defined as June, July and August) at the coolest (C3) and warmest  
513 (C10) sites in the Caerfanell sub-catchment of the Usk and one site on the  
514 main river (U2) from 1968 to 2013 (Figs 1a & 5b, d, f). There was a significant  
515 linear increase at all sites, although the 95% confidence intervals of the  
516 regression encompassed the overall mean maximum temperature at each  
517 site. For the coolest site (C3) the mean daily maximum temperature attained  
518 increased by 0.49 °C over 45 years (Fig. 5 b), though it remained a 'summer  
519 cool' stream (the daily maximum temperature never exceeded 15 °C), and for  
520 the warmest site (C10) it increased by 0.73 °C (Fig. 5 d). On the mainstem at  
521 U2 (Fig. 5 f), mean maximum temperature was higher than in the two  
522 headwater streams (Fig. 5 b & d), increasing by 1.03 °C from 1968 to 2013.  
523 Mean increases per decade at the three sites in the Usk system were thus  
524 0.1, 0.16 and 0.22 °C at C3, C10 and U2, respectively.

525

526 The Loire is unsurprisingly much warmer than the Usk, with summer  
527 mean maxima well over 20 °C at all three sites We modelled the same  
528 statistic (i.e mean daily maximum water temperature attained in summer) for  
529 three sites on the mainstem (Belleville, St. Laurent and Chinon; Fig. 1b & Fig  
530 5 a,c & e) for the period spanning the biological data (1989-2005). The very  
531 hot year 2003 stands out in these data. Overall, the modelled temperature  
532 increase (°C) from 1989 to 2005 was 0.63 (Belleville), 0.77 (St. Laurent) and  
533 1.23 (Chinon), but none of these increases were significant, perhaps because  
534 the period assessed was shorter than that for the Usk. Note that Moatar &  
535 Gaillard (2006) found a very long term increase in (partially modelled) annual  
536 mean water temperature in the middle-Loire of 0.8°C since 1881, and in  
537 measured increases in spring and summer between 1976 and 2003 that were  
538 markedly higher than that (1.5-2.0 °C). Over the period spanned by our  
539 biological data, the average decadal rate of increase in mean daily maximum  
540 summer temperature at Belleville, St. Laurent and Chinon (i.e. up-to

541 downstream) was 0.39, 0.48 and 0.77 °C, respectively, and were thus rather  
 542 greater than estimates for any site on the Usk system.



543  
 544

545 **Fig. 5** Modelled summer (June, July, August) mean daily maximum water  
 546 temperature at (a,c,e) three sites on the Loire (progressively downstream, see Fig.  
 547 1b), and (b,d,f) three sites in the Usk system (C3 and C10 in the headwaters, U2 in  
 548 the mainstem, Fig.1a). The Loire data span 1989-2005 and the Usk data 1968-2013.  
 549 Broken lines, show the overall mean maximum daily summer temperature over the  
 550 years between the biological surveys.

551

552 **Discussion**

553

554 There is no consistent evidence of any upstream movement among the  
 555 Hydropsychidae in either river, despite marginally significant increases in  
 556 summer maximum temperature at the Usk sites for which we have  
 557 information, and grounds to suspect temperature increases in the Loire. We  
 558 modelled summer temperature maxima because it was the feature of streams

559 that was most closely related to species distribution in the earlier data,  
560 probably through its influence on metabolic rate and oxygen requirements  
561 (Edington & Hildrew 1973; Hildrew & Edington 1979; Verberk et al. 2016).  
562 Furthermore, summer temperature is experienced by different aquatic life  
563 stages of the species (final instar larvae and pupae in early summer, eggs  
564 and young larvae later in the summer). Evidently, the increase in mean  
565 summer maxima in the Usk system was modest, about 0.1 °C per decade in  
566 the summer-cool *D. felix* site (C3), 0.16 °C per decade in the summer warm C  
567 10, a site with *H. instabilis* and *H. siltalai*, and 0.22 °C per decade in the main  
568 river at U2, a site with *H. siltalai*, *H. pellucidula* and, formerly, *H.*  
569 *contubernalis*. The Loire has warmed rather more quickly since around 1980,  
570 but certainly by less than 1 °C per decade in the middle reaches (in terms of  
571 summer maxima), and over the whole 20<sup>th</sup> century warmed much less rapidly  
572 than that (Moater & Gaillard, 2006). Moatar & Gaillard (2006) further found an  
573 important influence of declining river discharge in driving increases in river  
574 temperature in the Loire, consequent upon increases in water withdrawals  
575 and deficits in rainfall.

576

577 Data on changes in stream temperature from the UK uplands are still  
578 quite scarce. However, Durance & Ormerod (2007) estimated a rise in mean  
579 annual temperature of about 0.6 °C per decade and 0.7°C per decade in  
580 forested and moorland upland streams in mid-Wales, less than about 50 km  
581 distant from our sites in the Brecon Beacons. In continental Europe, Hari *et al.*  
582 (2006) reported an impressive Swiss data set of frequent measurements from  
583 25 sites from 1978 to 2002 over an altitudinal gradient of 4607m and found a  
584 regionally coherent increase in river temperature at all altitudes, that was  
585 abrupt in the late 1980s, with the persistent onset of consistently warmer  
586 springs. Webb & Nobilis (2007) analysed even longer records of river  
587 temperature from Austria, over the entire 20<sup>th</sup> century, and overall found clear  
588 evidence of increases broadly correlated with air temperature. They also  
589 found great variability among systems, with least warming in the headwaters,  
590 and even evidence of spring cooling at some sites between 1901 and 1990,  
591 though this was reversed in the warm final decade of the last century. In one  
592 of the longest continuous and most consistent empirical records of

593 temperature in a headwater stream, Schmidt (2011) found an increase in  
594 annual mean temperature of 0.85 °C over 37 years from 1969-2006 (0.23 °C  
595 per decade), in the Breitenbach, a spring-fed sandstone stream in central  
596 Germany.

597

598 Our estimates for the Usk system, based essentially on measurements  
599 in two years, coinciding with ecological assessments, and modelled over the  
600 intervening period of about 40 years, suggest a warming trend but apparently  
601 much more subdued than that estimated by Durance & Ormerod (2007), at  
602 least for the headwaters. This difference could be explained at least partially  
603 by difference in the period assessed, since temperature in the Central  
604 England record declined somewhat after 2007, following a shift in the North  
605 Atlantic Oscillation (UK Meteorological Office:  
606 <http://www.metoffice.gov.uk/hadobs/hadcet>). Our data do show remarkable  
607 local variation among sites, separated in some cases by <1km. Thus, sites  
608 C10 and C3 (Fig. 4) could be as much as 4°C different at any one instant and,  
609 perhaps not surprisingly, held different species. The sites differed in such  
610 aspects as distance from the source, aspect and vegetation cover, all of which  
611 are known to affect stream temperature (Caissie, 2006; Malcolm *et al.*, 2004;  
612 Webb *et al.*, 2008). This not only shows the high heterogeneity of stream  
613 temperature but suggests that thermal refugia may persist in future and that  
614 local management (including reinstatement of riparian woodland) could be  
615 effective (e.g. Gray & Edington, 1969; Thomas *et al.*, in press).

616

617 There could be a number of feasible, and not mutually exclusive,  
618 explanations for the persistence of the longitudinal distribution of  
619 hydropsychids in two river systems over fairly long periods of time. The first is  
620 that the temperature changes have not yet been sufficient to produce change  
621 detectable here. The second is that temperature has a lesser effect on  
622 distribution than expected. The third is that other factors, not part of climate  
623 change, play a contributory role that precludes, or counteracts, a simple shift  
624 in longitudinal distribution.

625



626           Nothing in our data from either river system suggests a change in  
627 distribution consistent with warming. From the Usk, the only deletion was of  
628 *Hydropsyche contubernalis* from the lowest reaches of the river. This was a  
629 species that we predicted would actually extend its range upstream as the  
630 river warmed, and the river itself did warm by  $>1^{\circ}\text{C}$  over the period. However,  
631 this species is also present in large continental rivers, as it is in the Loire, at  
632 temperatures exceeding anything it experiences in the Usk. The loss of *H.*  
633 *contubernalis* from the Usk, if it persists, must be ascribed to factors other  
634 than temperature. Its population size in the Usk, where it was formerly  
635 restricted to the very lowest reaches, must have always been rather small,  
636 and therefore as susceptible as any other marginal population to chance  
637 disturbances (e.g. Gaston 2003). We considered the possibility that an  
638 increase in the tidal influence, probably by temporarily restricting water flow at  
639 high tide rather than by saline incursions, might have occurred. Phillips &  
640 Crisp (2010) surveyed sea-level trends at a number of sites (including the  
641 town of Newport at the mouth of Usk) around the wider Severn Estuary, with  
642 data from 1993 to 2007 inclusive. They found an overall increase in mean sea  
643 level of  $2.4\text{ mm y}^{-1}$ , although this was accompanied by an apparent decline in  
644 maximum sea-level and an increase in minimum sea level, and thus with an  
645 overall reduction in tidal range. Within this period, however, was a period of  
646 four years early in the record (1995-1998) with very high maximum sea level  
647 and increased storminess, associated with a very negative NAO index,  
648 producing very high tides at the river mouth (Newport). Thus, there is some  
649 indication of periods of extreme tides, which might have deleterious effects on  
650 freshwater species living at the upstream tidal limit. The pupae of caddis could  
651 be particularly vulnerable to arrested flow (reduced water velocity and thus  
652 increased oxygen stress) through the pupal case at such times. Note also that  
653 temperature is related intimately with requirements for oxygen in aquatic  
654 insects. Thus, Verberk *et al.* (2016) recently found that the upper lethal  
655 temperature limits for two common mayflies (Ephemeroptera) were greatly  
656 reduced when oxygen supply was low and a combination of temperature and  
657 Biological Oxygen Demand significantly affected site occupancy. Set against  
658 this hypothesis, however, note that *Cheumatopsyche lepida* is similarly  
659 restricted to the lower reaches of the Usk and persists to the present.

660 Whatever the veracity of these speculations, however, no upstream  
661 movement of any species is apparent in either river

662

663 In terms of whether we would be able to detect any upstream shift in  
664 distribution, our sites in the headwaters of the Usk in particular were quite  
665 densely distributed, separated only by a few 10s of metres in altitude and by  
666 longitudinal distances of c 200 m in some instances. An upstream retreat of  
667 *Diplectrona felix*, therefore, should have been detectable, unless it was very  
668 slight indeed, and it was nearest the source in the Usk catchment that the  
669 temperature increase was least.

670

671 The circumstantial evidence that temperature plays a key role in the  
672 ecology of such poikilothermic animals seems very strong, and has long been  
673 studied by ecologists (Macan, 1963; Elliott 1994; Hildrew & Edington, 1979).  
674 However, there have been additional candidate explanations for the  
675 ubiquitous longitudinal patterns observed for lotic animals. Thus, Statzner &  
676 Higler (1986) argued that changes in hydraulic conditions along rivers drove  
677 species turnover and zonation patterns, and a great deal of research on  
678 stream hydraulics followed from that conjecture (e.g. Statzner, Gore & Resh,  
679 1988; Statzner & Borchardt, 1994; Méricoux & Dolèdec, 2004). More recently,  
680 Statzner *et al.* (2010) and Statzner & Dolèdec (2011), using both molecular  
681 and conventional (based on larval morphology) approaches, showed that  
682 there is a clear phylogenetic signal on the longitudinal distribution of European  
683 hydropsychids. Those close to their aquatic ancestors were distributed  
684 nearest the source with progressively 'younger' species further downstream.  
685 This was correlated with a suite of related adaptations including, in headwater  
686 species, ecophysiological traits suiting them to cool water, a high optimum  
687 water velocity for net-spinning, and coarse grains for building the pupal case.  
688 Thus the longitudinal distribution of species is a rather complex, multifactorial  
689 phenomenon with an evolutionary basis. This seems to confirm the earlier  
690 view (Ross, 1956; Wiggins & Wichard, 1989) that 'primitive' lineages of  
691 caddisflies are characteristic of cool, oxygen-rich headwaters, and are  
692 replaced by warm-adapted descendants downstream.

693

694 In the particular context of climate change, therefore, we may doubt that  
695 temperature increases alone would produce a simple shift upstream, since  
696 other key features of the environment, such as near-bed velocity, sediment  
697 grain size and shear stress, would not change in parallel with the climate.  
698 Temperature increase might thus cause a spatial physicochemical ‘mismatch’  
699 between favourable habitat features normally found together but now  
700 separated. This is analogous to the concept of a temporal mismatch, for  
701 instance between a consumer and its resources, brought about by warming  
702 (e.g. Stenseth & Mysterud, 2002; Edwards & Richardson, 2004). An inability  
703 to shift upstream with warming could then cause a reduction of growth  
704 efficiency and changes in phenology that may be deleterious, ultimately  
705 causing reductions in density or even local extinction. As a possible example  
706 of a species loss in streams driven by climate changes, Durance & Ormerod  
707 (2010) ascribed the local extinction of the cool-water triclad flatworm *Crenobia*  
708 *alpine* to the potential combined effects of a prolonged warm period and  
709 interspecific competition. It may not be safe to assume that species can  
710 simply find refuge from warming by moving upstream and this provides  
711 another potential explanation for the ‘failure’ of some species to move in the  
712 way expected.

713

714 In conclusion, it seems that either the temperature changes in these  
715 rivers have not (yet) been sufficient to drive a detectable change in distribution  
716 or, more alarmingly, that the animals may effectively be ‘rooted to the spot’  
717 and unable to move. Future observations would show whether distributional  
718 shifts do eventually become apparent if there is further warming, or whether  
719 there are reductions in density and/or species losses in this key group of river  
720 organisms, and potentially in others.

721

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723

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727

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729

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737

738

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992 **Table S1:** a) Number of individuals collected at 33 sites on the Loire in  
 993 1989, 1991, 1993 ('former survey')(Ivol. et al. 1997) and in 2005 ('recent  
 994 survey')(Statzner et al. 2010; Statzner & Dolèdec 2011) and at 31 sites in the  
 995 Usk catchment in 1968 and 1970 ('recent survey' (Hildrew, unpublished) and  
 996 in 2012 (this paper); b) mean abundance (nos. per 5 mins  $\pm$ 95% CL) in the  
 997 Usk system in 1968/70 and in 2012, plus *P*-values (**bold** *P*<0.05) from a U-  
 998 test comparing median abundances where the species occurred in the two  
 999 surveys.  
 1000 **a)**

Species/Acronym	Individuals	
	Former survey	Recent survey
<b>Loire</b>		
<i>H. bulgaromanorum</i> Malicky 1977/ <i>bul</i>	179	141
<i>H. contubernalis</i> McLachlan 1865/ <i>con</i>	1663	2743
<i>H. dinarica</i> Marinkovic 1979/ <i>din</i>	10	115
<i>H. exocellata</i> Dufour 1841/ <i>exo</i>	999	3709
<i>H. incognita</i> Pitsch 1993/ <i>inc</i>	406 <sup>1</sup>	842
<i>H. ornatula</i> McLachlan 1878/ <i>orn</i>	4	33
<i>H. siltalai</i> Döhler 1963/ <i>sil</i>	57	1437
<i>C. lepida</i> (Pictet 1834)/ <i>lep</i>	125	1283
	$\Sigma$ 3443 <sup>2</sup>	$\Sigma$ 10303 <sup>3</sup>
<b>Usk</b>		
<i>D. felix</i> (McLachlan 1878)/ <i>fel</i>	125	171
<i>H. instabilis</i> (Curtis 1834)/ <i>ins</i>	1723	417
<i>H. pellucidula</i> (Curtis 1834)/ <i>pel</i>	129	55
<i>H. siltalai</i> Döhler 1963/ <i>sil</i>	837	299
<i>C. lepida</i> (Pictet 1834)/ <i>lep</i>	10	3
	$\Sigma$ 2824	$\Sigma$ 945

1001 <sup>1</sup>Previously identified as *H. pellucidula* (Curtis 1834).

1002 <sup>2</sup>Material included 239 young larvae that could not be identify as species.

1003 <sup>3</sup>Material included 711 first instar larvae that could not be identify as species

1004 **b)**

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Species	Individuals		Comparisons
	Former survey	Recent survey	U-test
<b>Caerfanell-subcatchment</b>			
<i>fel</i>	9.8 $\pm$ 8.3	2.9 $\pm$ 1.8	0.123
<i>ins</i>	127.7 $\pm$ 116.7	20.0 $\pm$ 23.8	0.154
<i>sil</i>	11.8 $\pm$ 11.0	1.2 $\pm$ 2.1	<b>0.014</b>
<b>Tarell-subcatchment</b>			
<i>fel</i>	6.7 $\pm$ 4.0	21.1 $\pm$ 17.8	0.200
<i>ins</i>	71.6 $\pm$ 53.2	29.8 $\pm$ 26.2	0.093
<i>sil</i>	32.0 $\pm$ 34.7	13.4 $\pm$ 35.2	0.072
<b>River Usk mainstem</b>			
<i>pel</i>	16.1 $\pm$ 13.9	6.9 $\pm$ 3.3	0.113
<i>sil</i>	75.8 $\pm$ 62.2	28.1 $\pm$ 23.1	<b>0.027</b>

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