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

Running head: Persistent longitudinal distribution of lotic insects

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Abstract

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

Introduction

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

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

Apparent 'radiations' of related species, occupying habitats with different thermal regimes, have been described in a number of groups (e.g. Ide, 1935; Macan, 1961, 1963; Vannote & Sweeney, 1980). In some cases, there is evidence of physiological adaptations to temperature, which are thought to underlie the observed longitudinal distribution. A prominent example is a globally-distributed family of net-spinning caddis flies, the Hydropsychidae, whose abundant larvae are important ‘ecosystem engineers’ and suspension feeders in rivers and streams, increasing the retention nutrients and carbon within the river ecosystem (e.g. Wallace, Webster & Woodall, 1977; Albertson & Daniels, 2016). A number of researchers independently found that the respiratory physiology of various species in this family appears to match the thermal environment. Thus, Hildrew & Edington (1979) showed that *Diplectrona felix* is a species of extreme headwaters, being replaced downstream first by *Hydropsyche instabilis* and then by *Hydropsyche siltalai* and *Hydropsyche pellucidula* and others. This spatial pattern in one Welsh river was correlated with increasingly warm summer conditions, *D. felix* never occurring where the daily maximum in summer exceeded 15 ˚C (i.e. they were restricted to ‘summer cool’ streams). They also showed (Edington & Hildrew, 1973; Hildrew & Edington, 1979) that, in three of these species, resting metabolic rate was relatively independent of temperature under conditions that matched those of the respective river reaches occupied, and which they suggested maximised growth efficiency in nature. Similarly, Lowe & Hauer (1999) related the longitudinal distribution of two species of hydropsychids in the northern Rocky Mountains to river temperature, and again found that differences in the metabolic rate-temperature relationship were consistent with their longitudinal distribution. Further, Roux *et al*. (1992) showed that the ‘amplitude’ of metabolic rate over the range of environmental temperatures from 5 to 25 °C increased with stream order (increasing stream size) in five European species of *Hydropsyche* in the River Rhône. There is thus considerable circumstantial and experimental evidence of a key role for temperature in the longitudinal distribution of this group of insects, and therefore grounds to expect that the distribution might change with consistent warming.

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

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

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

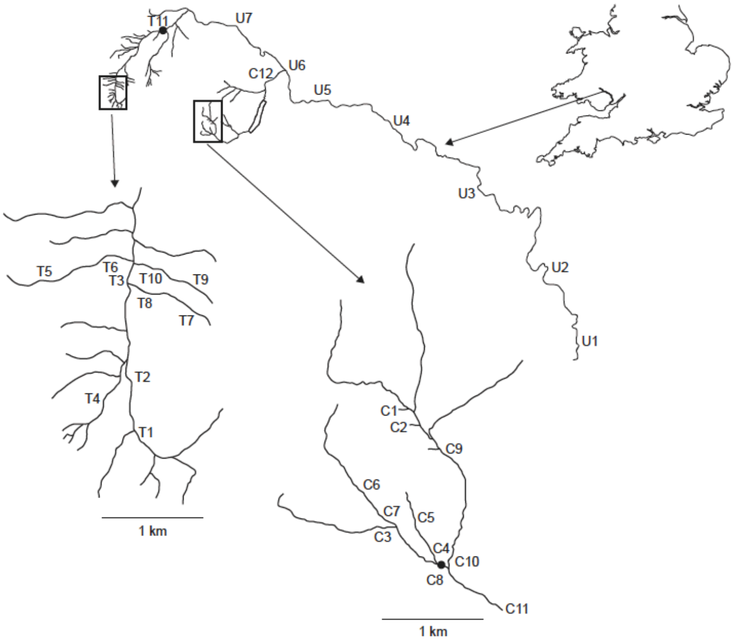
Opportunities to replicate previous studies after significant periods of time are relatively few and here we took advantage of earlier 'snapshot' surveys of the longitudinal distribution of hydropsychid larvae from two contrasting river systems, the Welsh Usk (assessed in 1968-1970; Hildrew & Edington, 1979) and the French Loire (assessed from 1989-1993; Ivol *et al.*, 1997). While the rivers are very different, the clear, and rather similar, distribution of hydropsychid larvae along both systems is an example of the classical sequential replacement of species in rivers (Hildrew & Edington, 1979; Statzner & Dolèdec, 2011), with which temperature (among other physical factors) has been implicated. We expected that water temperature would have increased in both systems and postulated that the distribution of species would have changed, as warm-adapted species from downstream moved further upstream and cool adapted species in headwaters retreated up the slope.

Methods

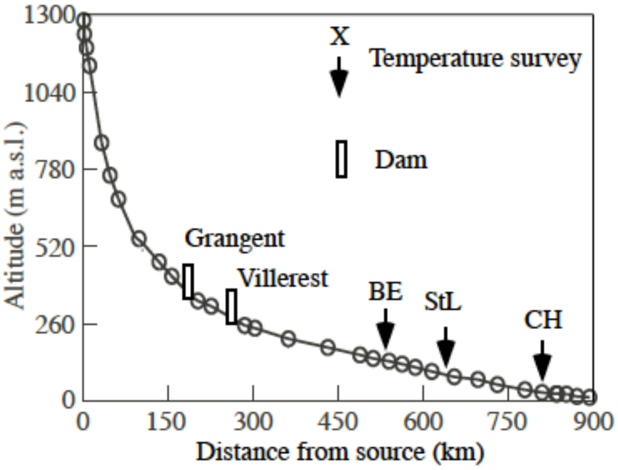
Site description

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

Sampling focussed on the main river and on two important south-bank headwaters (the Afon Tarell and the Caerfanell systems) of the Usk, draining the northern flanks and/or north-eastern flanks of the Brecon Beacons (a National Park in south Wales), with upland catchments of rough grazing with some semi-native woodland and coniferous forestry (Fig. 1a). These are typical upland stony/rocky streams with fast flowing water and channel widths up to about 4.5 m. Discharge, though permanent, is flashy and responds quickly to rainfall.



a)



b)

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

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

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

Species Distribution

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

There have been a number of surveys of hydropsychids in the Loire. Ivol *et al*. (1997) report collections from 38 sites in 1989, 1991 and 1993, while Statzner *et al*. (2010) and Statzner & Dolèdec (2011) sampled most of the same sites in 2005. We collate here data from 32 sites with accessible hydropsychid habitat on the Loire sampled by both teams (Fig. 1b) ranging from 1 to 893 km from the source in the Massif Central and over an altitudinal gradient of over 1200m. The sites are arranged in a simple longitudinal sequence downstream from the source. Ivol *et al*. (1997) describe searches using a hand-net (mesh 0.5mm) for 10 minutes at each site, brushing stones into a container and preserving the samples onsite and sorting and counting them in the laboratory. The later surveys were carried out by two people, picking up large stones and pieces of dead wood and brushing them into a similar hand-net for 20 minutes. Samples were again sorted and counted in the laboratory. Thus, surveys on the Loire, while using basically similar methods, were carried out by different teams and with differing intensity, so we compare these data only in terms of presence/absence and relative abundance.

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

Water temperature

The Usk

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

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

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

Since we had no measured data for the intervening years between the studies, we modelled monthly water temperature from monthly air temperature using sigmoid functions. Sigmoid functions are considered to be a better alternative to linear functions when using air temperature as the single independent variable to predict stream temperature (Mohensi *et al.*, 1998). Indeed, while linear regression analysis is widely used to model water from air temperatures (e.g. Stefan & Preud'homme, 1993; Durance & Ormerod 2007), it is recognized that, at extreme values of air temperatures, the relationship between daily water and air temperature departs from linearity. This is because, at high temperature, non linearity arises due to evaporative cooling (Mohensi *et al.*, 2002), while at low air temperature, non-linearity arises because water temperature is buffered by hyporheic and phreatic water and freezes only when air temperature drops significantly below 0°C (Crisp & Howson, 1982).

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

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

The Loire

For the Loire, we used the measured and modelled data of Electricité de France (EDF) (methods, data and modelling results courtesy of Dr Alain Poirel, EDF). The entire data set covered the period from 1949 to 2013. From these, we selected the period covered by our biological data (1989-2005). Here, we used the measured or modelled mean of the daily maximum water temperature for the three summer months (June, July, August) at locations upstream of three nuclear power plants distributed along the lower Loire (Fig. 1b). Where available, we used measured data and complemented periods with missing values using modelled data.

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

Results

Distribution

Five hydropsychid species were found on the Usk in both surveys, one species of *Diplectrona*, one of *Cheumatopsyche* and three in *Hydropsyche*, whereas one further species of *Hydropsyche* occurred only in the original survey and another only in the recent survey (Table 1a). In the Loire, eight species were taken in both surveys, seven species in *Hydropsyche* and one in *Cheumatopsyche*, while two further *Hydropsyche* species appeared in the more recent data only (Table 1b). Both studies included a substantial fraction of the hydropsychid fauna of both regions and all species known from both rivers were found in one or both surveys. The ‘densities’ (as numbers caught) differed between occasions in both the UK and French studies. In the Loire, more individuals were taken in the more recent survey for all species except *H. bulgaromanorum* (Table S1 in Supporting Information), which no doubt is largely accounted for by the greater sampling effort in the latter, so we could not test statistically for density differences in the two studies. In the Usk, where estimates were more comparable (see Methods), densities were not significantly different between the two studies, except those of *H. siltalai* in the Caerfanell and the main river, in both of which the species was less abundant in 2012 than in 1968/70 (Table S1).

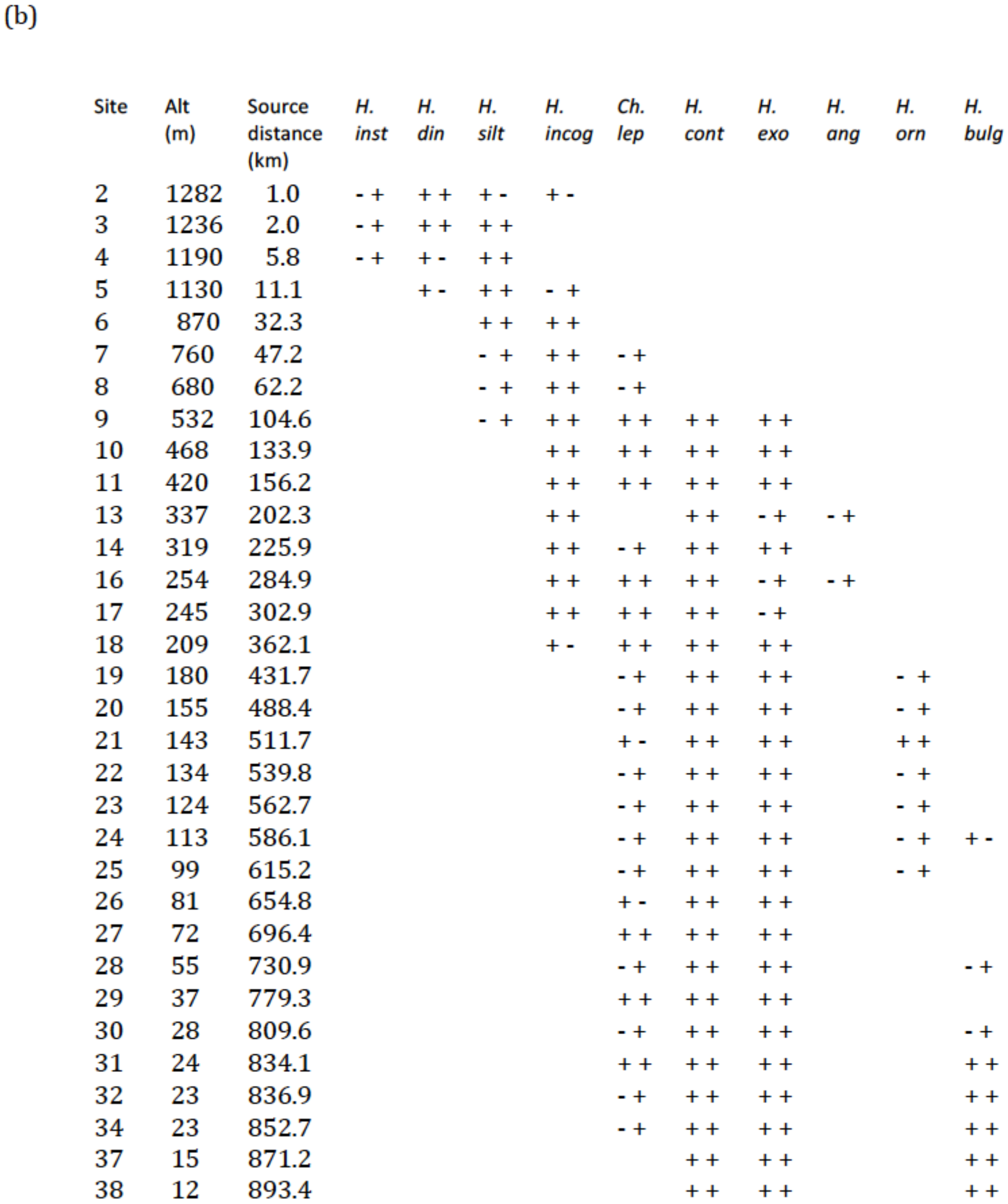
In terms of simple presence and absence, there were remarkably few changes in species complement in the Usk system between 1968/70 and 2012 (Table 1a). With one exception, all species present in the earlier samples were also taken at the same sites in 2012. The species most typical of larger rivers,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

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)	*D. fel*	*H. fulv*	*H. inst*	*H. silt*	*H. pell*	*H. cont*	*Ch. lep*
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)	*H. inst*	*H. din*	*H. silt*	*H. incog*	*Ch. lep*	*H. cont*	*H. exo*	*H. ang*	*H. orn*	*H. bulg*
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						+ +	+ +			+ +

In terms of the longitudinal distribution of relative abundances of the species (Fig. 2), in the Loire, the regression of the 50th percentile of the recent distribution of species on their former distribution shows that all species fall close to the x=y line (where there is no change) (Fig. 2b). The 25th percentile regression shows *Hydropsyche exocellata* falls outside the 95% CL, and that it was relatively more abundant upstream in the recent data, though there was no overall extension of its range (Table 1b) or any change in the position of its 50th or 75th percentile distribution. Thus, it was not found at sites 13, 16 and 17 in the previous data set (Table 1b). Conversely, the 75th percentile of the distribution of abundance of *Cheumatopsyche lepida* was further downstream in the recent data, consistent with its more widespread occurrence at sites in

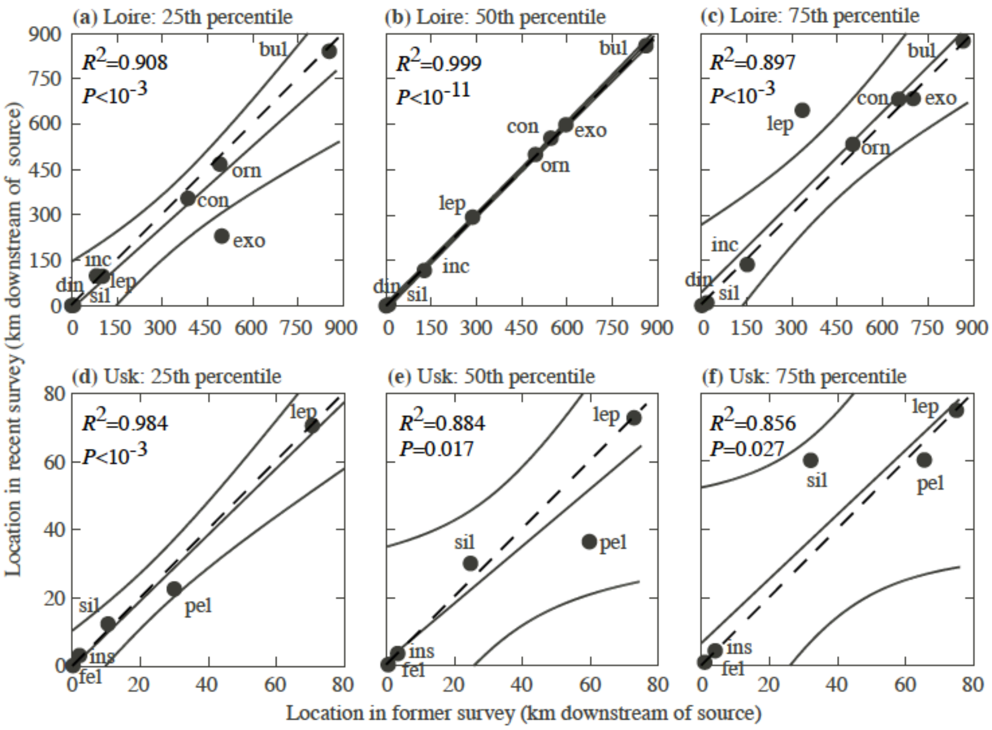


Fig. 2 Plots of the 25th, 50th and 75% percentiles of the cumulative relative abundance of hydropsychid species in (a,b,c, respectively) the Loire and (d,e,f, respectively) the Usk, comparing the ‘old’ (x) and ‘new’ (y) data. Points show the position (km downstream) at which 25, 50 or 75% of the final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

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

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

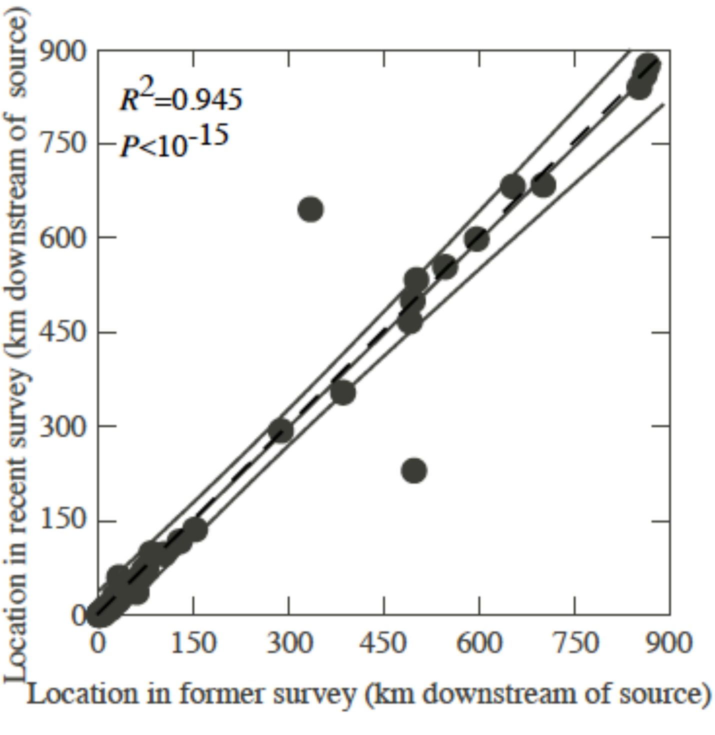


Fig. 3 Points for the 25th, 50th and 75th percentiles of the cumulative relative abundance of all species in both rivers from Fig. 2 analysed in one regression (see

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

Temperature

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

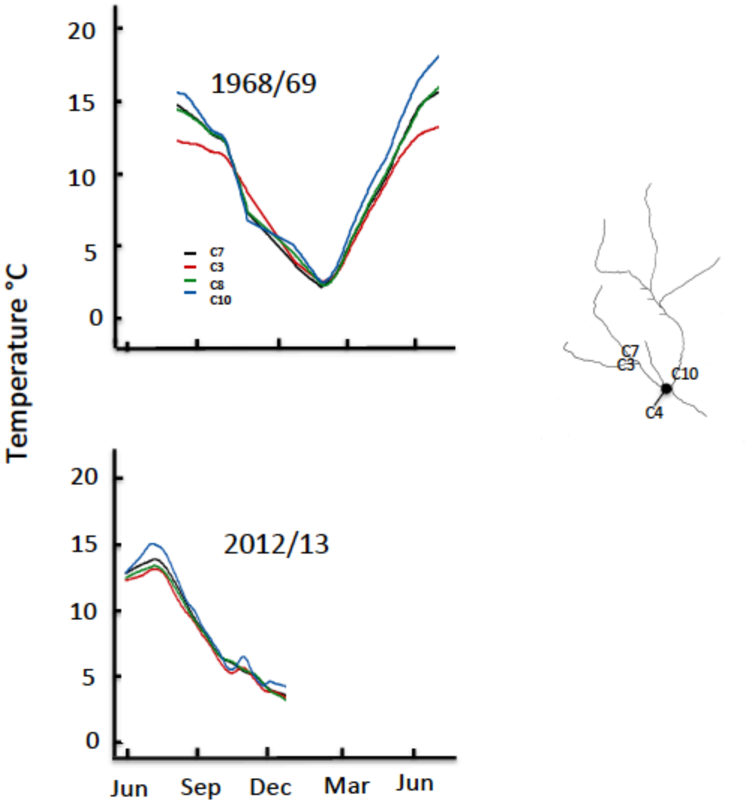


Fig. 4 Smoothed (Lowess) plots of measured daily maximum stream temperature at four sites in the Caerfanel sub-catchment of the Usk (inset, C7, C3, C8 and C10; Fig. 1a) in 1968/69 and for the first half of 2012/13.

We modelled the mean daily maximum stream temperature attained in summer (defined as June, July and August) at the coolest (C3) and warmest (C10) sites in the Caerfanell sub-catchment of the Usk and one site on the main river (U2) from 1968 to 2013 (Figs 1a & 5b, d, f). There was a significant linear increase at all sites, although the 95% confidence intervals of the regression encompassed the overall mean maximum temperature at each site. For the coolest site (C3) the mean daily maximum temperature attained increased by 0.49 °C over 45 years (Fig. 5 b), though it remained a 'summer cool' stream (the daily maximum temperature never exceeded 15 °C), and for the warmest site (C10) it increased by 0.73 °C (Fig. 5 d). On the mainstem at U2 (Fig. 5 f), mean maximum temperature was higher than in the two headwater streams (Fig. 5 b & d), increasing by 1.03 °C from1968 to 2013. Mean increases per decade at the three sites in the Usk system were thus 0.1, 0.16 and 0.22 °C at C3, C10 and U2, respectively.

The Loire is unsurprisingly much warmer than the Usk, with summer mean maxima well over 20 °C at all three sites We modelled the same statistic (i.e mean daily maximum water temperature attained in summer) for three sites on the mainstem (Belleville, St. Laurent and Chinon; Fig. 1b & Fig 5 a,c & e) for the period spanning the biological data (1989-2005). The very hot year 2003 stands out in these data. Overall, the modelled temperature increase (°C) from 1989 to 2005 was 0.63 (Belleville), 0.77 (St. Laurent) and 1.23 (Chinon), but none of these increases were significant, perhaps because the period assessed was shorter than that for the Usk. Note that Moatar & Gaillard (2006) found a very long term increase in (partially modelled) annual mean water temperature in the middle-Loire of 0.8°C since 1881, and in measured increases in spring and summer between 1976 and 2003 that were markedly higher than that (1.5-2.0 °C). Over the period spanned by our biological data, the average decadal rate of increase in mean daily maximum summer temperature at Belleville, St. Laurent and Chinon (i.e. up-to downstream) was 0.39, 0.48 and 0.77 °C, respectively, and were thus rather greater than estimates for any site on the Usk system.

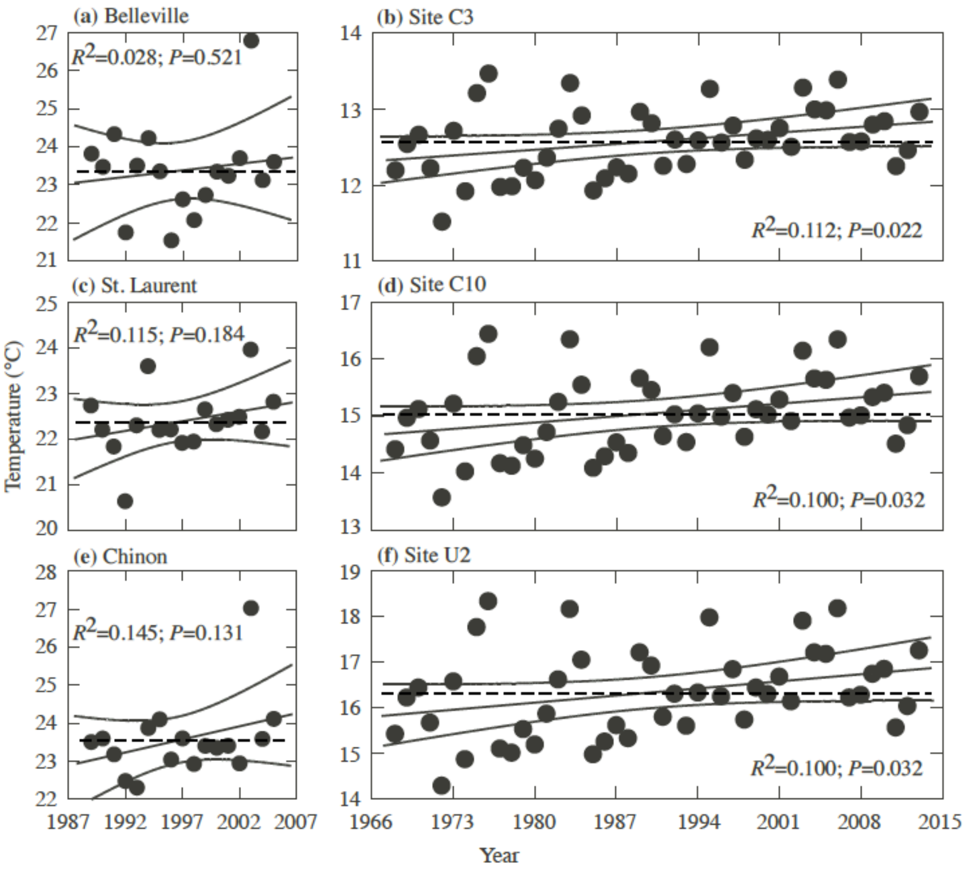


Fig. 5 Modelled summer (June, July, August) mean daily maximum water temperature at (a,c,e) three sites on the Loire (progressively downstream, see Fig. 1b), and (b,d,f) three sites in the Usk system (C3 and C10 in the headwaters, U2 in the mainstem, Fig.1a). The Loire data span 1989-2005 and the Usk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

Discussion

There is no consistent evidence of any upstream movement among the Hydropsychidae in either river, despite marginally significant increases in summer maximum temperature at the Usk sites for which we have information, and grounds to suspect temperature increases in the Loire. We modelled summer temperature maxima because it was the feature of streams that was most closely related to species distribution in the earlier data, probably through its influence on metabolic rate and oxygen requirements (Edington & Hildrew 1973; Hildrew & Edington 1979; Verberk et al. 2016). Furthermore, summer temperature is experienced by different aquatic life stages of the species (final instar larvae and pupae in early summer, eggs and young larvae later in the summer). Evidently, the increase in mean summer maxima in the Usk system was modest, about 0.1 °C per decade in the summer-cool *D. felix* site (C3), 0.16 °C per decade in the summer warm C 10, a site with *H. instabilis* and *H. siltalai*, and 0.22 °C per decade in the main river at U2, a site with *H. siltalai*, *H. pellucidula* and, formerly, *H. contubernalis*. The Loire has warmed rather more quickly since around 1980, but certainly by less than 1 °C per decade in the middle reaches (in terms of summer maxima), and over the whole 20th century warmed much less rapidly than that (Moater & Gaillard, 2006). Moatar & Gaillard (2006) further found an important influence of declining river discharge in driving increases in river temperature in the Loire, consequent upon increases in water withdrawals and deficits in rainfall.

Data on changes in stream temperature from the UK uplands are still quite scarce. However, Durance & Ormerod (2007) estimated a rise in mean annual temperature of about 0.6 °C per decade and 0.7°C per decade in forested and moorland upland streams in mid-Wales, less than about 50 km distant from our sites in the Brecon Beacons. In continental Europe, Hari *et al*. (2006) reported an impressive Swiss data set of frequent measurements from 25 sites from 1978 to 2002 over an altitudinal gradient of 4607m and found a regionally coherent increase in river temperature at all altitudes, that was abrupt in the late 1980s, with the persistent onset of consistently warmer springs. Webb & Nobilis (2007) analysed even longer records of river temperature from Austria, over the entire 20th century, and overall found clear evidence of increases broadly correlated with air temperature. They also found great variability among systems, with least warming in the headwaters, and even evidence of spring cooling at some sites between 1901 and 1990, though this was reversed in the warm final decade of the last century. In one of the longest continuous and most consistent empirical records of temperature in a headwater stream, Schmidt (2011) found an increase in annual mean temperature of 0.85 °C over 37 years from 1969-2006 (0.23 °C per decade), in the Breitenbach, a spring-fed sandstone stream in central Germany.

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

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

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

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

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

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

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

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

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

a)

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

[1] Previously identified as *H. pellucidula* (Curtis 1834).

[2] Material included 239 young larvae that could not be identify as species.

[3] Material included 711 first instar larvae that could not be identify as species

b)

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

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