This item was submitted to [Loughborough's Research Repository](#) by the author.
Items in Figshare are protected by copyright, with all rights reserved, unless otherwise indicated.

Detecting phenology change in the mayfly *Ephemera danica*: responses to spatial and temporal water temperature variations

PLEASE CITE THE PUBLISHED VERSION

<http://dx.doi.org/10.1111/een.12164>

PUBLISHER

Wiley Publishing / © The Royal Entomological Society

VERSION

AM (Accepted Manuscript)

PUBLISHER STATEMENT

This work is made available according to the conditions of the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International (CC BY-NC-ND 4.0) licence. Full details of this licence are available at:
<https://creativecommons.org/licenses/by-nc-nd/4.0/>

LICENCE

CC BY-NC-ND 4.0

REPOSITORY RECORD

Everall, Nicholas C., Matthew F. Johnson, Robert L. Wilby, and Cyril J. Bennett. 2019. "Detecting Phenology Change in the Mayfly *Ephemera Danica*: Responses to Spatial and Temporal Water Temperature Variations". figshare. <https://hdl.handle.net/2134/17672>.

Detecting phenology change in the mayfly *Ephemera danica*:
Responses to spatial and temporal water temperature variations

Nicholas C. Everall,¹ Matthew F. Johnson², Robert L. Wilby² and Cyril J. Bennett¹

¹ Aquascience Consultancy, 18 Hawthorne Way, Ashgate, Chesterfield, Derbyshire S42 7JS,
UK. Email: rnaquaconsult@aol.com

² Department of Geography, Loughborough University, Leicestershire, LE11 3TU, UK.
Email: m.f.johnson@lboro.ac.uk; r.l.wilby@lboro.ac.uk

Corresponding author: Nicholas Everall, rnaquaconsult@aol.com

Accepted for publication: *Ecological Entomology*

Date of acceptance: 16 September 2014

Abstract

1. Rising water temperatures under climate change are expected to affect the phenology of aquatic insects, including the mayfly *Ephemera danica* which is widespread throughout Europe.

2. To assess temporal and spatial variability in mayfly emergence, *E. danica* were monitored at two thermally contrasting reaches in the River Dove, English Peak District over the period 2007 to 2013. Inter-annual variations in growing degree days (GDDs) were modelled for an upstream site with intermittent spring flow supplementing main channel flow (Beresford Dale) and downstream site dominated by near constant discharges of cool groundwater (Dovedale).

3. A strong association exists between the emergence cycle of *E. danica* and GDDs at each site. Beresford Dale accumulated on average 374 more GDDs than Dovedale. Following warm summers *E. danica* emerged after only one year in Beresford Dale but began to revert to a bi-annual cycle after the particularly wet/cool year of 2012. In Dovedale, *E. danica* maintained a two-year cycle throughout the monitoring period despite the phenology changes observed 8 km upstream.

4. Data from the present study suggest that habitats near cool groundwater may provide important refugia for populations of insects, potentially delaying permanent shifts in phenology under climate change. However, ability to detect changes in the thermal triggers and phenological response may be hindered by conventional spot sampling protocols.

Keywords: Mayfly; Phenology; Water temperature; Emergence; Thermal refugia

INTRODUCTION

Water temperature (T_w) affects many aspects of aquatic life including the metabolism of animals (e.g. Weatherley & Ormerod, 1990) and photosynthesis of plants (Berry & Björkman 1980). Insects are poikilothermic ectotherms so their development and phenology are regulated by ambient temperatures (Raddum & Fjellheim, 1993; Knispel *et al.*, 2006). Development ceases when T_w is outside upper or lower thresholds, and thermal extremes can cause stress or even mortality (Dallas & Rivers-Moore, 2012). Consequently, cumulative or growing degree days (GDDs) are often used to relate thermal conditions to organism development (Neuheimer & Taggart, 2007). GDDs are the number of degrees that exceed a minimum temperature threshold each day, accumulated over the development period or year.

Insect phenology is extremely diverse, often very plastic, and characterised by individuals progressing through multiple, distinct life-stages. Timing of emergence from aquatic larval stage to the sexually mature, terrestrial stage is of particular significance because many insects have only a short window to mate and lay eggs. It is, therefore, important that emergence coincides with favourable weather and is synchronous, both as a population defence against predation and as a means of maximising potential genetic spread (Watanabe *et al.*, 1999; Sparks *et al.*, 2010).

River temperature is spatially heterogeneous and temporally variable (Webb *et al.* 2008). Water temperatures usually have strong diel and seasonal cycles related to solar forcing, and typically increases with distance downstream. Tributaries and groundwater can interrupt this pattern and create locally distinct thermal regions. For example, phreatic groundwater usually has a relatively constant temperature that reduces diel and seasonal temperature ranges (Constantz, 1998; O'Driscoll & DeWalle, 2006).

There is evidence that river Tw is changing in response to climate change (van Vliet *et al.*, 2011; Isaak *et al.*, 2012; Orr *et al.* 2014). In addition, land drainage, alteration of river courses and ponding by weirs, can alter the thermal dynamics of rivers (Caissie, 2006), as can removal of riparian vegetation (e.g. Broadmeadow *et al.*, 2011). Aquatic organisms respond to changing thermal conditions in complex ways (Ward & Stanford, 1982). Given the dependence of phenology on heat accumulation, emergence of insects is particularly susceptible to changing temperature and can have adverse effects on freshwater insects populations (Harper & Peckarsky, 2006; Durance and Ormerod, 2007; Thackeray *et al.*, 2010). In this paper, we describe spatial and temporal variability in mayfly emergence in the River Dove, English Peak District. We then assess links between varying Tw and mayfly phenology, and discuss whether conventional monitoring protocols are adequate for detecting changes in the thermal driver and ecological response.

MATERIALS AND METHODS

Study organism

Ephemera danica Muller, 1764 (Ephemeroptera) is one of the largest mayflies found in the British Isles with some females reaching over 30 mm. The larvae are burrowing animals and are often found where silt accumulates in rivers. Traditionally *E. danica* has been reported to emerge after two years in an aquatic nymphal stage and is referred to as a semivoltine species (Wright *et al.*, 1981; Tokeshi, 1985; Elliott *et al.*, 1988). The adult emergence period is normally in late-May and early-June. Tokeshi (1985) found that male *E. danica* have a minimum growth threshold of 2.6 °C and require at least 3398 annual GDDs to emerge. Females have a higher minimum growth threshold (3.1 °C) and hence require more GDDs for

emergence (3631). Differing growth thresholds for males and females is common in mayfly populations (Svensson 1977; Wright *et al.* 1981).

In controlled laboratory experiments, Bennett (2007) noted that both male and female *E. danica* can reach maturity in a single year with larvae reaching up to 19 mm within four months from hatching when Tw averages 20 °C. Bennett (2007) also noted that *E. danica* in the North Wey, Surrey, UK reached maturity in a single year between 1995 and 2002. The current study builds on these observations by examining the life cycle of *E. danica* from 2007 to 2013 at two contrasting sites in the River Dove, UK.

River Dove and sampling sites

The River Dove rises on Axe Edge from moorland springs and runs southward for 73 km through the Peak District National Park before joining the River Trent at Newton Solney. The catchment area upstream of monitoring sites is 131 km² and elevation ranges from 450 m at source to 155 m in Dovedale. Land-use is predominately grazed pasture with isolated stands of deciduous woodland covering 5% of the catchment. Annual precipitation exceeds 1000 mm. The Dove flows parallel to a Carboniferous limestone outcrop with phreatic springs, which it intersects at Beresford.

Invertebrate and Tw monitoring sites are located in Beresford Dale and Dovedale (Figure 1). Beresford Dale is 20 km from the source of the Dove, situated at the upstream end of a limestone gorge. Here, intermittent springs discharge water of relatively constant temperature (9–14 °C) during autumn and winter. Dovedale is 9.7 km downstream of Beresford Dale in a limestone gorge with Ash (*Fraxinus excelsior*) woodland. Here, groundwater discharges into the river all year-round at ~8.5 °C. The stretch between Beresford and Dovedale is affected

by over 100 weirs (< 0.5 m high) installed over a century ago to increase the feeding area for trout. The Environment Agency of England and Wales (EA) have recorded daily discharge at a gauging station in Dovedale since 1969 (Figure 1).

Water temperature monitoring and analysis

The Loughborough University TEMperature Network (LUTEN) consists of 36 monitoring sites in the Rivers Dove and Manifold. At each site, Gemini Aquatic 2 *Tinytag* thermistors record the maximum, mean and minimum air and T_w every 15-minutes since March 2011. *Tinytag* thermistors have a quoted accuracy of $0.2\text{ }^{\circ}\text{C}$, which has been confirmed under experimental conditions (Johnson & Wilby, 2013). There are eight LUTEN sites between invertebrate monitoring sites (Figure 1). Sites D16 (Beresford Dale) and D24 (Dovedale) are the closest records. However, D24 has an incomplete record due to sensor failure and as such, D23 is used herein, which records almost identical temperatures to D24 (maximum difference in daily temperature was $0.62\text{ }^{\circ}\text{C}$ during model calibration and validation period). Full details of LUTEN, the monitoring strategy and data validation can be found in Wilby *et al.* (2012) and Johnson *et al.* (2014).

The EA takes monthly spot measurements for routine monitoring. To test the ability of this sampling strategy to detect thermal changes one value per month was randomly selected from the 15 minute LUTEN data during typical EA sampling hours (08:00 to 18:00) from June 2011 to May 2012. These 12 values were then used to estimate the annual mean at site D16. This was repeated 1000 times allowing estimation of the variance in the mean due to daylight sample times, when compared with the ‘true’ estimate based on the full LUTEN-record.

Water temperatures for the years 2007 to 2013 were hindcast from air temperatures measured at Buxton, Derbyshire (~20 km from study sites and significantly correlated ($r^2 = 0.8$) to 3-years of monitored air temperature at each site). Air and water temperature are not directly related but because both are ultimately driven by solar radiation, the latter can be predicted from air temperatures using regression analysis (Stefan and Preud'homme, 1993; Mohseni *et al.*, 1998). We deploy logistic regression models built previously for LUTEN sites and tested under contrasting weather conditions (Johnson *et al.* 2014; Wilby *et al.*, 2014). These models explained 85% of the variance in Tw at D16 and 83% at D23 (Table 1) and have the form:

$$Tw = \frac{\alpha}{(1 + \exp^{\gamma(\beta - Ta)})} \quad (1)$$

where α is the model asymptote, β is the model inflection point and γ is the model gradient at β . Using the same models, a Tw record was constructed for 2005–2013 in order to calculate GDDs using the thresholds of Tokeshi (1985). GDDs were accumulated from 1 June to the 31 May each year to match the normal development period of *E. danica* from egg-laying.

Invertebrate sampling

Invertebrate monitoring sites were approximately 40 m long, 7–8 m wide, and located in riffles. Two sites in Beresford Dale were 100 m downstream of Hartington bridge and approximately 100 m apart. The substrate consists of clean, coarse-gravels (median grain size [D_{50}]=48 mm) and sparse stands of water crowfoot (*Ranunculus* spp.) with very occasional starwort (*Callitriche* spp.). The Dovedale site also comprises of clean, coarse-gravels (D_{50} =41 mm) with sparse weed-beds of water crowfoot (*Ranunculus* spp.).

All study reaches hold good populations of *E. danica* based on data collected from previous surveys (Everall, 2010; 2012). *E. danica* samples were taken from exposed gravels and fine-sediment beneath weed-beds using a 0.1 m² Surber net sampler fitted with a 2 cm deep steel curtain. Sampling was undertaken in Aprils 2007, 2010, 2011, 2012 and 2013 following the life-stage techniques of Bennett (2007). The number of *E. danica* individuals and their body length was recorded by site and year. Mayflies larger than 7 mm were also sexed; this was not always possible for smaller individuals.

In a two-year cycle it is expected that there will be a tri-modal size distribution with separate peaks for male and female adults about to emerge in June, and a third peak of smaller mayflies that require an additional year of growth. Male and female mayflies usually form distinct size classes because of the differing GDDs required for development. In a one year cycle, mayfly samples are expected to have a uni-modal size distribution with the majority about to emerge in June plus a few smaller, over-wintering individuals (Figure 2). Hence, the number of small, unsexed mayfly present each year, and the size difference between males and females, are indicators of the presence of the two-year emergence cycle.

Statistical analysis

SPSS 19.0 was used for all regression analysis. Statistical comparison between the total length of male and female mayflies between and within years was undertaken with Mann-Whitney U tests in SPSS 19.0.

RESULTS

Variations in water temperature

Daily-mean Tw has clear seasonality in Beresford Dale (Figure 3). Year 2006 was the warmest in the monitoring period and amongst the hottest on record in the UK. Hindcast annual mean Tw varied by no more than 1.0 °C between consecutive years, but GDDs fell between 2006 and 2010 before rising in 2011 and 2012 (Table 2). However, summer GDD increased between 2008 and 2011. Overcast conditions and high discharge resulted in markedly lower summer Tw in 2011–2012 even though the annual GDDs were the second highest. Observed Tw were under-predicted in summer 2011 but over-predicted by the model in 2012, because of the changing significance of spring flow contributions which are not fully replicated by the model (Figure 3). At Dovedale, annual mean Tw was less variable between years and the seasonal range is less than at Beresford due to groundwater inflows (Table 2). Consequently, summer temperatures are relatively cool and there were on average, 260 fewer GDDs each year between 2006 and 2011 (Figure 3). The contrast between Beresford Dale and Dovedale was greatest in the summer. For example, in 2012–2013 there were 266 more GDDs in Beresford Dale of which 231 were due to higher summer temperatures (Table 2).

The EA spot sampling yields Tw mean 10.3 ± 1.1 °C ($n=12$) compared with the resampled LUTEN Tw mean 9.5 ± 0.01 °C in Beresford Dale (Figure 4), whereas the entire LUTEN record yields Tw mean 9.7 ± 0.02 °C ($n=32160$).

Temporal variations in emergence

In 2007, *E. danica* at Beresford Dale had a tri-modal size distribution, with larger males and females about to emerge plus a third group of smaller mayflies (Figure 5a). Monitoring in 2010 revealed a uni-modal size distribution indicating a single year cohort (Figure 5b). Mayfly with body length >22 mm may be a remnant cohort of second year females. However, the lack of a second generation indicated by smaller, unsexed individuals, and lack of size

distinction between the sexes, suggest emergence mostly within one year of hatching. This pattern continued in 2011 and 2012 with few small (<10 mm) mayflies (Figure 5b).

In 2013, the nymph populations in Beresford Dale appeared to be reverting back to a two year, tri-modal size distribution (Figure 5b). The presence of small individuals (<8 mm) suggests over-wintering mayflies and the greater distinctiveness between males and females is indicative of a two year cohort (Table 3). This apparent reversion back to a two-year cycle coincides with the cool summer and low GDDs of the previous year (Figure 6a).

In 2011, adult male and female mayflies were on average 11.1 mm and 11.5 mm long, respectively (compared with 18.0 mm and 23.7 mm in 2007). This is statistically different in both cases (Mann-Whitney U; $p < 0.001$) (Figure 6). The distribution of mayfly sizes was also significantly different between years, indicated by Levene's tests ($p < 0.001$ for both males and females), with 2007 populations of male and female being less varied than in 2010 and 2011. In Beresford Dale, females were significantly larger than males within all years, except 2011 when sexes were statistically similar (see Table 3 for p -values). In Dovedale, females were statistically distinct from males in both years.

The one year cohorts between 2010 and 2012 coincided with warmer summers and the return to a bi-annual cohort in 2013 with the unusually cool summer of 2012. As expected, the average size depends on the number of GDDs over the preceding year with mayfly larger when emerging after a warm year (Figure 6). In addition, mayflies developing in one year are generally smaller than those with a two year generation because more GDDs are accumulated over two moderately warm years than one very warm year. However, the relatively warm year 2011 produced large mayfly, despite the fact that the population had a one year generation period (Figure 6).

222 *Spatial variations in emergence*

223 The *E. danica* population in Dovedale is unlike that in Beresford Dale during the same year
224 (Figure 7). Populations in Dovedale retained a large number of small, unsexed mayfly in
225 2012 and 2013, in comparison to none (2012) and six (2013) in Beresford. Males and females
226 also formed distinct size classes, in contrast to Beresford Dale where there was substantial
227 overlap (although in 2013 there was some divergence between size of males and females).

228 *E. danica* sampled in Dovedale were generally larger than those in Beresford even though
229 male mayflies in Dovedale were exposed on average to 374 fewer GDDs between 2005 and
230 2011. However, the contrast in thermal regime between the two sites was reduced in 2012–
231 2013 when Dovedale had 266 fewer GDDs (Table 2). It should also be noted that because
232 mayflies in Dovedale retained two year generations, they actually accumulated substantially
233 more GDDs than those in the warmer sites of Beresford.

234 **DISCUSSION**

235 *Plasticity in phenology*

236 In 2007 at Beresford Dale, *E. danica* nymphs entering a second year largely accounted for
237 good recruitment the following year but, by 2010–2012 the mayfly population appeared to be
238 supplemented by nymphs reaching maturity in a single year. This is consistent with studies of
239 *E. danica* in southern England chalk streams showing that both males and females can reach
240 maturity in a single year depending on Tw (Bennett, 2007). Field data from the River Dove
241 suggests that summer maximum temperatures above 15 °C result in *E. danica* moving
242 towards a one year cohort. These results are consistent with temperature thresholds in both
243 field and laboratory studies (Bennett, 2007). Thermal dynamics in the River Dove were
244 related to changing river flow during the monitoring period with high summer temperatures

in 2011 associated with drought conditions and low temperatures in 2012 with exceptionally wet conditions (Parry et al. 2013). Other studies have tested the phenological response of mayfly (*Baetis bicaudatus*) to both temperature and discharge and found that temperature accelerated emergence but flow had no impact (Harper & Peckarsky 2006).

E. danica phenology in the River Dove appears to be plastic, changing temporally from year-to-year. GDDs proved more useful in generalising thermal regimes than annual mean temperature. River temperatures in preceding summer and autumn strongly determine subsequent emergence patterns. Bennett (2007) also found that summer-autumn was the critical period influencing *E. danica* development and summer temperatures have been identified as significant to other mayfly species (*Ephoron shigae*, Watanabe *et al.*, 1999) and insect groups including stonefly, caddisfly and beetles (Haidekker & Hering 2008; Li *et al.*, 2011). As far as the authors are aware, the apparent change in *E. danica* populations in the River Dove from a one year cycle in 2012 back to two year cycle in 2013 is the first documented evidence of a reversal in mayfly phenology related to Tw. This reversal was associated with cooler summer (and annual) Tw in Beresford Dale. In other words, a short-term reduction in thermal exposure coincided with a phenology reversal in *E. danica*.

Mayflies grew larger, more were caught, and there was greater distinctiveness in size between the sexes when exposed to higher GDDs. Conversely, mayflies were smaller, less numerous and the size of males and females were more alike when developing over fewer GDDs. However, this relationship was complicated because fewer GDDs were accumulated when developing over a single hot year in comparison to two cooler years. Consequently, mayflies emerging in a one-year cycle, associated with warm years, were smaller than those emerging after two relatively cool years, consistent with the findings of Bennett (2007).

269 *Implications of changing mayfly phenology*

270 The phenology of many insect species has been related to temperature, in terms of timing of
271 emergence, size of emerging individuals, and generation period (see Thackeray et al., 2010).
272 Phenology changes could be of significance because populations with single year cycle are
273 potentially more vulnerable to adverse weather when the majority of the population is in
274 terrestrial, adult form (Bennett, 2007). For example, prolonged high winds and heavy rain
275 during the main emergent period in 2000 prevented female *E. danica* with a mainly one-year
276 generation on the River Wey, Surrey from returning to the water to lay eggs (Bennett &
277 Gilchrist, 2010). As a result, the larval population was much reduced the following year,
278 whereas a large population remained in the River Test in Hampshire where larvae had
279 maintained a predominately two year cycle (Bennett & Gilchrist, 2010). In other words,
280 populations with a two year cycle have a reserve of over-wintering individuals that
281 supplement emergence in the following year.

282 Water temperature has also been related to the size and fecundity of adults in a number of
283 species (see reviews in Honêk 1993; Blanckenhorn, 2005). Consequently, altering the growth,
284 development and size of insects may impact population dynamics by affecting reproductive
285 success. Hence, smaller mayflies emerging from a one year cycle in the Dove are likely to
286 have less reproductive success than larger mayflies emerging after two years development.
287 This has been confirmed in *E. danica* by Bennett (1996) who found smaller females produced
288 fewer eggs than larger individuals: ~6000 in 24 mm females, compared with ~3000 in 18 mm
289 females. Consequently, mayflies in the River Dove at Beresford in 2010 and 2011 are likely
290 to have produced fewer than half the eggs of mayfly in Dovedale over the same time period.

291 Given the dependence of insect development on heat accumulation through larval stages, it is
292 likely that phenology changes have occurred during warm periods in the climate record.

However, the negative connotations associated with one-year emergence cycles combined with long-term warming of freshwaters (particularly in summer) suggests that anthropogenic climate change could have adverse impacts on mayfly phenology. In addition, the differing size and abundance of mayfly between years could affect trophic relationships, altering food availability and food-web dynamics. However, the spatial heterogeneity in mayfly phenology in the Dove might act to buffer against mayfly shortages at a site because predatory birds and fish could move to other sites where mayfly populations may be larger.

Management of thermal refugia

E. danica populations at sites A and B (separated by 300 m) in Beresford Dale were very similar. However, the phenology of mayflies from Beresford Dale and Dovedale (separated by 8.4 km) were substantially different. Dovedale is fed by considerable groundwater inflows, which lower mean Tw with dampened seasonal and diel cycles (Johnson et al. 2014). The cooler water of the River Dove (especially in summer) appears to have provided a thermal refuge where *E. danica* phenology has remained unchanged compared to Beresford Dale. Such areas could be of critical ecological significance in the context of climate change because they could delay changes in insect phenology. Conversely, warming reaches could experience substantial changes in phenology.

Given the implications of rising Tw for insect populations, it is important to understand and attempt to manage river temperatures. Spot sampling of daytime Tw 12-times a year, following the sampling strategy of the EA, over-estimated annual mean Tw relative to continuous monitoring and the standard error of the EA estimate (1.1 °C) is comparable to the difference between warmest and coolest years in the LUTEN hindcast series (1.6 °C). It is further recognised that any creep in spot sampling time, for example, from early-morning to

midday, could artificially increase Tw estimates (Toone et al. 2011). Moreover, annual Tw were poor indicators of thermal regime relevant to *E. danica*, as summer Tw was of greater importance. Consequently, spot sampling would have been insufficient to resolve differences in thermal regime between years or sites. Higher resolution sampling is needed to relate ecological changes to Tw, at least accounting for seasonal variations in temperature and preferably including sub-daily temperature changes which may be relevant to nocturnal fauna (Wilby et al., 2014). Reliable, sub-daily resolution temperatures can now be obtained via robust, field-deployable thermistors.

Regulatory bio-monitoring in the UK typically involves identifying invertebrates to family level for water quality and ecological assessment (Murray-Bligh, 1999; Environment Agency, 2009). Given the species-specificity of insect-temperature relationships it is important that finer resolution information is obtained when evaluating the impacts of changing thermal regime on invertebrates. Furthermore, monitoring schemes usually focus on invertebrate community composition (Paisley *et al.*, 2007). Whilst Tw may alter community composition, this is likely to be preceded by shifts in the growth, development and phenology of insects. Consequently, consideration of insect size and sex ratios within species would allow the identification of thermal effects before the loss of species from the community pool. Such metrics could be used for early climate change detection.

CONCLUSIONS

The phenology of *E. danica* was found to be highly plastic in the River Dove due to variations in summer Tw over the years 2007-2013. In addition, *E. danica* phenology varied between sites with and without permanent groundwater inflows. Changes in phenology can be detrimental to insect populations because of reduced fecundity and increased vulnerability

to adverse weather. Annual mean Tw can mask important thermal characteristics, particularly increasing summer temperatures, which correlate with *E. danica* emergence. In addition, high-resolution invertebrate monitoring (size of individuals within an individual species) was required to identify the impacts of changing Tw on *E. danica* populations. Routine, coarse-scale biomonitoring is unlikely to have detected such trends. An unusually cool summer in 2012 returned mayfly phenology to a two-year cycle. Consequently, the protection of thermal refugia (such as those areas where phraetic groundwater or riparian shade buffers against solar forcing) could buffer against phonological change in insects subject to rising Tw under climate change. In addition, artificial creation or enhancement of thermal refugia by riparian shade management could delay, or even reverse, changes to the phenology of some species otherwise impacted by higher water temperatures.

ACKNOWLEDGEMENTS

The authors wish to thank The Wild Trout Trust, Beresford Fishery, Derbyshire County Angling Club, Peak District National Park Authority and Staffordshire Wildlife Trust for part-funding this work. The opinions expressed by the authors do not necessarily reflect those of the aforementioned organisations. The manuscript was improved in response to the helpful comments of two anonymous reviewers.

Contribution of authors

Everall and Johnson designed the project. Everall and Bennett collected and analysed invertebrate data. Johnson and Wilby collected and analysed temperature data. All authors contributed to paper writing.

364

365 **REFERENCES**

366 Bennett CJ. (1996) The ecology of mayflies (Ephemeroptera) in the upper reaches of the
367 River Wey in Surrey. PhD thesis, University of London, UK (unpublished).

368 Bennett CJ. (2007) The ecology of a seven year study of the life cycle of the mayfly
369 *Ephemera danica*. *Freshwater Forum* **27**: 3–14.

370 Bennett CJ, Gilchrist W. (2010) Riverflies. In: Maclean, N. (ed) *Silent Summer*. Cambridge
371 University Press, UK. pp. 401–414.

372 Berry J, Bjorkman O. (1980) Photosynthetic response and adaptation to temperature in higher
373 plants. *Annual Review of Plant Physiology* **31**: 491–543.

374 Blanckenhorn WU. (2005) Behavioral causes and consequences of sexual dimorphism.
375 *Ethology* **111**: 977–1016.

376 Broadmeadow SB, Jones JG, Langford TEL, Shaw PJ, Nisbet TR. (2011) Influence of
377 riparian shade on lowland stream water temperatures in southern England and their viability
378 for brown trout. *River Research and Applications* **27**: 226–237.

379 Caissie D. (2006) The thermal regime of rivers: a review. *Freshwater Biology* **51**: 1389–1406.

380 Constantz J. (1998) Interaction between stream temperature, streamflow, and groundwater
381 exchanges in alpine streams. *Water Resources Research* **34**: 1609–1615.

382 Dallas HF, Rivers-Moore NA. (2012) Critical thermal maxima of aquatic macroinvertebrates:
383 towards identifying bioindicators of thermal alteration. *Hydrobiologia* **679**: 61–76.

384 Durance I, Ormerod SJ. (2007) Climate change effects on upland stream macroinvertebrates
 385 over a 25-year period. *Global Change Biology* **13**: 942–957.

386 Elliott JM, Humpesch UH, Macan TT. (1988) *Larvae of the British Ephemeroptera. A key*
 387 *with ecological notes*. Scientific Publication No. 49. Freshwater Biological Association.
 388 Ambleside.

389 Environment Agency (2009) *Freshwater Macro-invertebrate Analysis of Riverine Samples*.
 390 Operational Instruction 024_08. Environment Agency, UK.

391 Everall NC. (2010) The aquatic ecological status of the rivers of the Upper Dove Catchment
 392 in 2009. *Natural England Commissioned Report NECR046*. Natural England: Sheffield.

393 Everall NC, Farmer A, Heath AF, Jacklin TE, Wilby RL. (2012). Ecological benefits of
 394 creating messy rivers. *Area* **44**: 470–478.

395 Gurnell A, Tockner K, Edwards P, Petts G. (2005) Effects of deposited wood on
 396 biocomplexity of river corridors. *Frontiers in Ecology and Environment* **3**: 377–382.

397 Haidekker A, Herring D. (2008) Relationship between benthic insects (Ephemeroptera,
 398 Plecoptera, Coleoptera, Trichoptera) and temperature in small and medium-sized streams in
 399 Germany: A multivariate study. *Aquatic Ecology* **42**: 463–481.

400 Harper MP, Perckarsky BL. (2006) Emergence cues of a mayfly in a high-altitude stream
 401 ecosystem: Potential response to climate change. *Ecological Applications* **16**: 612–621.

402 Honêk A. (1993) Intraspecific variation in body size and fecundity in insects: a general
 403 relationship. *Oikos* **66**: 483–492.

404 Imholt C, Gibbins CN, Malcolm LA, Langan S, Soulsby C. (2010) Influence of riparian
 405 cover on stream temperatures and the growth of the mayfly *Baetis rhodani* in an upland
 406 stream. *Aquatic Ecology* **44**: 669–678.

407 Isaak DJ, Wollrab S, Horan D, Changler G. (2012) Climate change effects on stream and
 408 river temperatures across the northwest U.S. from 1980–2009 and implications for
 409 salmonid fishes. *Climate Change* **113**: 499–524.

410 Johnson MF, Wilby RL. (2013) Shield or not to shield: Effects of solar radiation on water
 411 temperature sensor accuracy. *Water* **5**: 1622–1637.

412 Johnson MF, Wilby RL, Toone JA. (2014) Inferring air-water temperature relationships
 413 from river and catchment properties. *Hydrological Processes* **28**: 2912–2928.

414 Knispel S, Sartori M, Brittain JE. (2006) Egg development in the mayflies of a Swiss glacial
 415 floodplain. *Journal North American Benthological Society* **25**: 2, 430–443.

416 Li JL, Johnson SL, Sobota JB. (2011) Three responses to small changes in stream
 417 temperature by autumn-emerging aquatic insects. *Journal of the North American*
 418 *Benthological Society* **30**: 474–484.

419 Mohensi O, Stefan HG, Erickson TR. (1998) A nonlinear regression model for weekly stream
 420 temperatures. *Water Resources Research* **34**: 2685–2692.

421 Murray-Bligh JAD. (1999) *Procedure for collecting and analysing macro-invertebrate*
 422 *samples*. Quality Management Systems for Environmental Biology: Biological Techniques,
 423 BT001 Version 2.0. Bristol: Environment Agency.

424 Neuheimer AB, Taggart CT. (2007) The growing degree-day and fish size-at-age: the
 425 overlooked metric. *Canadian Journal of Fisheries and Aquatic Science* **64**: 375–385.

426 O'Driscoll MA, DeWalle DR. (2006) Stream-air temperature relations to classify stream-
 427 ground water interactions in a karst setting, central Pennsylvania, USA. *Journal of Hydrology*
 428 **329**: 140–153.

429 Paisley MF, Trigg DJ, Walley WJ. (2007) Revision and Testing of BMWP scores. Final
 430 report SNIFFER Project WFD72a. Edinburgh, UK.

431 Parry S, Marsh T, Kendon M. (2013) 2012: from drought to floods in England and Wales.
 432 *Weather* **68**: 268–274.

433 Raddum GG, Fjellheim A. (1993) Life-cycle and production of Baetis-Rhodani in a regulated
 434 river in Western Norway-comparison of pre-regulation and post-regulation conditions.
 435 *Regulatory Rivers Reservoir Management* **8**: 49–61.

436 Sparks TH, Preston CD, Roy DB. (2010) Climate Change. In: Silent Summer The State of
 437 Wildlife in Britain and Ireland. Ed. N. Maclean. Cambridge University Press, 765pp.

438 Stefan HG, Preud'homme EB. (1993) Stream temperature estimation from air temperature.
 439 *Water Resource Research* **29**: 27–45.

440 Svensson B. (1977) Life cycle, energy fluctuations and sexual differentiation in Ephemera
 441 Danica (Ephemeroptera), a stream-living mayfly. *Oikos* **29**: 78–86.

442 Thackeray SJ, Sparks TH, Frederiksen M, Burthes S, Bacon PJ, Bell JR, Botham MS,
 443 Brereton TM, Bright PW, Carvalho L, Clutton-Brock T, Dawsons A, Edwards M, Elliott M,
 444 Harrington R, Johns D, Jones ID, Jones JT, Leech DI, Roy DB, Scott WA, Smith M,
 445 Smithers RI, Winfield IJ, Wanless S. (2010) Trophic level asynchrony in rates of
 446 phonological change for marine, freshwater and terrestrial environments. *Global Change*
 447 *Biology* **16**: 3304–3313.

448 Tokeshi M. (1985) Life-cycle and production of the burrowing mayfly, *Ephemera danica*: a
 449 new method of estimating degree-days for growth. *Journal of Animal Ecology* **54**: 919–930.

450 Toone JA, Wilby RL, Rice SP. (2011) Surface-water temperature variations and river
 451 corridor properties. *Water Quality: Current Trends and Expected Climate Change Impacts*
 452 Proceedings of symposium H04 held during IUGG2011 in Melbourne, Australia, July 2011.
 453 IAHS Publication **348**; 129–134.

454 van Vliet MTH, Ludwig F, Zwolsman JJG, Weedon GP, Kabat P. (2011) Global river
 455 temperatures and sensitivity to atmospheric warming and changes in river flow. *Water*
 456 *Resources Research* **47**: 10.1029/2010WR009198.

457 Ward JV, Stanford JA. (1982) Thermal responses in the evolutionary ecology of aquatic
 458 insects. *Annual Review of Entomology* **27**: 97–117.

459 Watanabe NC, Mori I, Yoshitaka I. (1999). Effect of water temperature on the mass
 460 emergence of the mayfly, *Ephoron shigae*, in a Japanese river (Ephemeroptera:
 461 Polymitarcyidae). *Freshwater Biology* **41**: 537–541.

462 Weatherly NS, Ormerod SJ. (1990). Forest temperatures of upland streams in Wales: a
 463 modelling exploration of the biological effects. *Freshwater Biology* **24**: 109–122.

464 Webb BW, Hannah DM, Moore RD, Brown LE, Nobilis F. (2008) Recent advances in stream
 465 and river temperature research. *Hydrological Processes* **22**: 902–918.

466 Wilby RL, Orr H, Watts G, Battarbee RW, Berry PM, Chadd R, Dugdale SJ, Dunbar MJ,
 467 Elliott JA, Extence C, Hannah DM, Holmes N, Johnson AC, Knights B, Milner NJ, Ormerod
 468 SJ, Solomon D, Timlett R, Whitehead PJ, Wood PJ. (2010). Evidence needed to manage

469 freshwater ecosystems in a changing climate: Turning adaptation principles into practice.
 470 *Science of the Total Environment* **408**: 4150-4164.

471 Wilby RL, Johnson MF, Toone JA. (2012) The Loughborough University TEMperature
 472 Network (LUTEN): Rationale and analysis of stream temperature variations. *Proceedings of*
 473 *Earth Systems Engineering 2012: Systems Engineering for Sustainable Adaptation to Global*
 474 *Change*. Newcastle, UK.

475 Wilby RL, Johnson MF, Toone JA. (2014) Nocturnal river water temperatures: Spatial and
 476 temporal variations. *Science of the Total Environment* **482-483**: 157–173..

477 Wright JF, Hiley PD, Berrie AD. (1981). A nine-year study of the life cycle of *Ephemera*
 478 *danica* Müller. (Ephemeridae: Ephemeroptera) in the river Lambourn, England. *Ecological*
 479 *Entomology* **6**: 321–331.

480

Table 1 Logistic regression model parameters (α , β and γ), the amount of explained variance (r^2) and the standard error of the estimate (SE) in both calibration and validation periods, where SE is the RMS of error about the model, giving an estimate of the difference between observed and modelled values.

<i>Site</i>	Calibration (2011)					Validation (2012)	
	α °C	β °C	γ °C	r^2	SE °C	r^2	SE °C
Beresford	23.4	15.0	0.1	0.85	1.3	0.83	1.9
Dovedale	13.5	4.5	0.1	0.83	0.8	0.80	1.5

Table 2 Mean water temperature and GDDs in Beresford Dale and Dovedale. Annual (1 June to 31 May each year) and seasonal GDDs are also shown for summer (June to July); autumn (September to November); winter (December to February); and spring (March to May).

<i>Year</i>	Beresford Dale						Dovedale					
	Mean (°C)	Cumulative degree days					Mean (°C)	Cumulative degree days				
		ANN	JJA	SON	DJF	MAM		ANN	JJA	SON	DJF	MAM
2005/06	10.0	2697	1017	735	352	593	8.9	2305	749	616	398	542
2006/07	10.9	3038	1105	783	446	704	9.4	2495	781	643	461	610
2007/08	10.1	2749	967	692	455	634	9.0	2369	733	601	468	568
2008/09	9.8	2642	983	653	325	682	8.9	2293	738	578	377	599
2009/10	9.8	2615	1004	708	265	638	8.8	2260	745	610	332	572
2010/11	10.1	2705	998	647	329	731	8.9	2311	744	570	376	621
2011/12	10.3	2796	966	769	403	658	9.1	2483	731	668	432	682
2012/13	9.3	2426	958	614	334	520	8.4	2160	727	557	379	498

Table 3 The number (n) of male, female and small, unsexed mayfly and the percentage total each constitutes each year. The mean, median, maximum and minimum total lengths for male, female and unsexed individuals are included along with *p*-values from Mann-Whitney U tests between male and female sizes. The number of GDD preceding emergence over 1 and 2 years are quoted, along with the expected number of years emerging mayfly have developed over

		Beresford Dale							Dovedale	
		2007	2008	2009	2010	2011	2012	2013	2012	2013
Male	<i>n</i>	70			48	61	279	101	53	56
	%	20			32	27	48	47	27	19
	Mean	18.0			14.4	11.1	14.7	10.8	18.7	16.0
	Max	22			18.5	17	20	19	20.5	19
	min	14.5			9	8	9	8.5	15.5	14
Female	<i>n</i>	132			101	163	308	78	60	120
	%	37			68	73	52	37	30	41
	Mean	23.7			18.1	11.5	20.5	13.8	24.3	22.4
	Max	28			27	17.5	28	28	26.5	26
	min	19.5			9.5	6.5	13	11.5	21.5	19.5
<i>p</i> -value		<0.01			<0.01	0.496	<0.01	<0.01	<0.01	<0.01
Unsexed	<i>n</i>	156			0	0	0	34	86	115
	%	44			0	0	0	16	43	40
	Mean	3.6			0	0	0	7.5	4.3	6.5
	Max	5.5			0	0	0	8	7.5	10.5
	min	1			0	0	0	6	1	2.5
1-year GDD		3038	2749	2642	2615	2705	2796	2426	2483	2160
2-years GDD		5735	5787	5391	5257	5320	5501	5222	4794	4643
Expected life-cycle		2			1	1	1	2	2	2

Figure 1 The River Dove catchment showing invertebrate (green circles), LUTEN (red circles) and Environment Agency river gauge (black circle) sites. Grey indicates limestone outcrop; unshaded is millstone grit. Insets show Beresford Dale and Dovedale invertebrate sampling areas and closest LUTEN sites.

Figure 2 Schematic of the *E. danica* life-cycle. From hatching, larvae develop as they accumulate heat during their aquatic stage. Females grow larger than males over the same period and this variance widens as heat accumulates. Emergence occurs in early-June. Year 2 shows two cohorts with distinct male and female size distributions in one, and a group of small mayfly in their first year of growth. Year 4 shows a single year cohort, with mayflies about to emerge all of moderate size and males and females of similar dimensions. The transition between one and two year cycles (Year 3) also has no peak in small mayfly.

Figure 3a) Hind cast daily-mean Tw at Beresford Dale (red) and Dovedale (black) for June 2005 to May 2013. Model residuals are shown for Beresford Dale (pink) and Dovedale (grey) for the period with LUTEN data (March 2011 to May 2013). b) GDDs for years beginning in June 2005 to May 2013 at Beresford Dale (red) and Dovedale (black) assuming minimum growth threshold for male *E. danica* (2.6 °C).

Figure 4 Estimated annual mean temperatures at D16 (Beresford) based on 1000 replicates of one sample per month drawn from 15-minute LUTEN data for the hours 08:00 to 18:00. The overall LUTEN mean is shown by the vertical line. Shading denotes standard deviations from the mean.

Figure 5 Number and size of mayflies caught in Beresford Dale in a) April 2007 and b) each April from 2010 to 2013.

Figure 6a) Annual GDDs for growth threshold 2.6 °C (red line) and number of small mayfly (<7 mm) sampled each year (purple line) in Beresford Dale. b) Average length of female (left) and male (right) *E. danica* with 95% confidence intervals sampled in Beresford Dale (blue) and Dovedale (green). The red line indicates GDDs at Beresford for growth threshold of 2.6 °C. All years were statistically distinct for females.

Figure 7 Number and length of *E. danica* caught in Beresford Dale (left) and Dovedale (right) in 2012 and 2013.