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Keywords:	Climate , discharge , long-term study, river, salmon, stream, temperature, trout.
Abstract:	Widespread decline among Atlantic salmon (<i>Salmo salar</i>) and brown trout (<i>Salmo trutta</i>) over recent decades have been linked to pollution, exploitation and catchment modification, but climate change is increasingly implicated. We used long-term, geographically extensive data from the Welsh River Wye, formerly a major salmon river, to examine whether climatically-mediated effects on juveniles (> 0+) might contribute to population change. Populations of Atlantic salmon and brown trout fell across the Wye catchment respectively by 50% and 67% between 1985 and 2004, but could not be explained by pollution because water quality improved during this time. Stream temperatures, estimated from calibrations against weekly air temperature at 8 sites, increased by 0.5-0.7 °C in summer and 0.7-1.0 °C in winter, with larger tributaries warming more than shaded headwaters. Rates of winter warming were slightly greater after accounting for the effect of the North Atlantic Oscillation (1.1-1.4 °C). However, warming through time was smaller than measured variations among tributaries, and alone was insufficient to explain variations in salmonid density. Instead, population variations were best explained in multi-level mixed models by a synoptic variate representing a trend towards hotter, drier summers, implying interactions between climate warming, varying discharge and fluctuations in both brown trout and salmon.

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	Taken alongside recent data showing effects of warming on survival at sea, these data suggest that Atlantic salmon might be jeopardised by future climatic effects in both their marine and freshwater stages. Effects on non-diadromous brown trout also imply climatically mediated processes in freshwaters or their catchments. Climate projections for the UK suggest that altered summer flow and increasing summer temperatures could exacerbate losses further in these species, and we advocate management actions that combine reduced abstraction with enhanced riparian shading



For Review Only

Juvenile salmonid populations in a temperate river system track synoptic trends in climate

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Running head: *Climate and salmonids*

Abstract

Widespread decline among Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) over recent decades have been linked to pollution, exploitation and catchment modification, but climate change is increasingly implicated. We used long-term, geographically extensive data from the Welsh River Wye, formerly a major salmon river, to examine whether climatically-mediated effects on juveniles (> 0+) might contribute to population change.

Populations of Atlantic salmon and brown trout fell across the Wye catchment respectively by 50% and 67% between 1985 and 2004, but could not be explained by pollution because water quality improved during this time.

Stream temperatures, estimated from calibrations against weekly air temperature at 8 sites, increased by 0.5-0.7 °C in summer and 0.7-1.0 °C in winter, with larger tributaries warming more than shaded headwaters. Rates of winter warming were slightly greater after accounting for the effect of the North Atlantic Oscillation (1.1-1.4 °C). However, warming through time was smaller than measured variations among tributaries, and alone was insufficient to explain variations in salmonid density. Instead, population variations were best explained in multi-level mixed models by a synoptic variate representing a trend towards hotter, drier summers, implying interactions between climate warming, varying discharge and fluctuations in both brown trout and salmon.

Taken alongside recent data showing effects of warming on survival at sea, these data suggest that Atlantic salmon might be jeopardised by future climatic effects in both their

marine and freshwater stages. Effects on non-diadromous brown trout also imply climatically mediated processes in freshwaters or their catchments. Climate projections for the UK suggest that altered summer flow and increasing summer temperatures could exacerbate losses further in these species, and we advocate management actions that combine reduced abstraction with enhanced riparian shading.

Keywords: Climate, discharge, long-term study, river, salmon, stream, temperature, trout.

For Review Only

42 Introduction

43 Populations of Atlantic salmon (*Salmo salar*) and trout (*Salmo trutta*) have declined in
44 recent decades across large parts of their range (Slaney *et al.*, 1996; Parrish *et al.*, 1998;
45 Beamish *et al.*, 1999; Environment Agency 2003a). However, the factors involved remain
46 poorly understood despite large research efforts (Marschall and Crowder, 1996; Slaney *et al.*
47 *al.*, 1996; Armstrong *et al.*, 2003; Milner *et al.*, 2003; Ormerod, 2003). Particular
48 difficulties arise in migratory salmonids because life cycles in many species are divided
49 between marine and freshwater environments, where different effects operate. In
50 addition, abundance reflects both density-independent processes, such as habitat loss or
51 pollution, and also density-dependent feedbacks, such as territorial competition (Milner *et al.*
52 *al.*, 2003; Zabel *et al.*, 2006).

53 Key population factors almost certainly act in combination (Marschall and Crowder,
54 1996; Parrish *et al.*, 1998; Milner *et al.*, 2003), with density-dependence, environmental
55 or demographic stochasticity, and land or river management all implicated in current
56 declining trends in salmonid populations (Wilzbach *et al.*, 1998; Parrish *et al.*, 1998;
57 Ormerod, 2003; Zabel *et al.*, 2006). Effects might also be scale-dependent. At river reach
58 scales, habitat quality influences the abundance of salmonids by direct provision of
59 refugia and food resources, so that riparian or in-stream degradation can affect local
60 carrying capacity (Borsuk, *et al.*, 2006). More widely, across river catchments, barriers
61 to migration, habitat fragmentation, diffuse pollutants, agricultural intensification and
62 industrialization have all had negative effects (Parrish *et al.*, 1998; Ormerod, 2003; Suttle
63 *et al.*, 2004; Dudgeon *et al.*, 2006). Finally, over regional scales, direct exploitation and
64 disease can alter salmonid populations (Bowker *et al.*, 1998; Hari *et al.*, 2006; Quinn *et al.*

al., 2006). Commercial fishing of Atlantic salmon has occurred extensively across near-shore areas of Europe, including Ireland and the UK, and mortality from fishing has previously been implicated in decline (Common Fisheries Policy, Council Regulation 2371/2002/EC; Potter, *et al.*, 2003). Evidence from angling catches suggests that salmonid populations in rivers have not always recovered followed the reduction and closure of commercial net fisheries in the UK over the last two decades, although this is likely confounded by declining angler participation (Arahamian *et al.* 2009).

Speculation is now growing that the reduction of salmonid populations across regions must involve even broader-scale pressures than those outlined above, and climatic variations are implicated increasingly. Climate affects salmonids through precipitation and water temperature, with consequences for growth, development, behaviour and survival both in freshwater and marine stages (e.g. Flebbe *et al.*, 2006; Seo *et al.*, 2006; Walsh and Kilsby 2007; Taylor 2008). In addition, reductions in flow can reduce the accessibility of habitats and affect species' survival and distributions (Armstrong *et al.*, 2003; Hakala and Hartman, 2004; Riley, *et al.*, 2009). Similarly, increased stream temperatures may restrict the availability of thermal refugia in these typically cool-water fishes (Eaton *et al.* 1995; Breau, *et al.*, 2007). At sea, rising sea-surface temperature is a factor in population change (Beamish *et al.*, 1999; Beaugrand and Reid, 2003; Tolimieri and Levin, 2004; Todd *et al.* 2008). While much attention has focused on directional climate change the North Atlantic Oscillation (NAO) is also linked to changes in fish production and ecology in both marine and freshwater ecosystems (Elliott *et al.* 2000; Bradley and Ormerod, 2001; Parsons and Lear, 2001). Inter-annual variations in climate

87 – for example through drought – can also have large effects on salmonids (Elliott *et al.*
88 1997)

89

90 Although long-term data sets are increasingly available through which explanations for
91 variations among salmonids might be assessed, long-term evaluations of climatic effects
92 through time or between years are still few (Thomas, 1996; Bjornstad and Grenfell, 2001;
93 Daufresne *et al.*, 2004; Hulme, 2005; Crozier and Zabel, 2006). This is particularly the
94 case where species with and without marine phases in their life cycle, such as Atlantic
95 salmon and brown trout, have been compared in the same catchment. The River Wye, in
96 Wales, western Britain, provides a particularly important case study that allows an
97 evaluation of trends in both these species. [Here, brown trout are non-anadromous, unlike](#)
98 [some other UK rivers where this species has sea-run components, thus enabling a contrast](#)
99 [with migratory salmon \(Edwards and Brooker, 1982\).](#) The Wye was traditionally one of
100 the best salmon angling rivers in the UK, so that long-term and wide scale data on
101 juvenile populations are available (Gee, Milner and Hemworth 1978a,b). However, in
102 recent decades, there have been marked declines in stocks of Atlantic salmon and brown
103 trout (Gee and Milner, 1980; Gough *et al.*, 1992; Environment Agency, 2003 a and b).
104 Because riparian and in-stream management to benefit salmonids has been attempted, and
105 some aspects of water quality have improved, there are few local, catchment-scale factors
106 that might explain this decline (Clews and Ormerod 2009; Clews, Vaughan & Ormerod
107 2010).

108

Here, we identify large-scale environmental correlates with trends and fluctuations in the density of Atlantic salmon and brown trout across the Wye system over a 20-year period from 1984. Specifically, we test the hypotheses that i) densities of juvenile brown trout and Atlantic salmon have declined across the Wye catchment and ii) trends are better explained by climatic factors, rather than local water quality and iii) migratory Atlantic salmon are equally tied to climatic effects as are brown trout, which might be expected if climatic effects on freshwaters are important in salmonid trends.

Study Area

The River Wye, in temperate western Britain, rises at 677m OD (52° 28' N, 3° 45' W) before flowing south eastwards to join the Severn Estuary (Figure 1). Typical of upland, high-velocity rivers in the UK, the Wye dominantly drains a mix of rough grazing, pastoral agriculture, and deciduous woodland or forest plantation, while arable farming predominates in the lower Wye valley (Edwards and Brooker, 1982). The general ecology, land use and water quality have been described extensively (Edwards and Brooker, 1982; Ormerod and Edwards, 1987; Jarvie *et al.* 2003; Clews and Ormerod, 2009). The temperate climate means that precipitation averages around 912mm per annum across the catchment, although the precipitation volumes increase towards the north and west (Hughes and Morley, 2000) to 2500mm per annum (Jarvie *et al.*, 2003; NERC, 2005). Typical annual mean temperatures range from 8-11 °C, and the highest monthly means reach c 19 °C.

132 Partly because of its importance for Atlantic salmon the Wye river system is both a Site
133 of Special Scientific Interest (SSSI) and Special Area of Conservation (SAC) under the
134 EU Habitats Directive (Directive 92/43/EEC) (Joint Nature Conservancy Committee,
135 2004).

136 **Materials and Methods**

137 *Overall study design*

138 Trends in salmonid populations between 1985 and 2004 were assessed from 41 of the
139 Wye's tributaries, while hydrochemical and climatic correlates with fish density were
140 appraised on 27 tributaries from which chemical data were available. Fish population data
141 were used to investigate trends in salmonid populations through time and also to whether
142 trends were catchment-wide.

143

144 *Salmonid data*

145 Juvenile salmonid data were derived by electrofishing by the Environment Agency,
146 Wales (Environment Agency and CEFAS, 2004) during summer (April to October) most
147 frequently in August (61% of samples). Since post young-of-the-year (> 0+) survival,
148 unlike young-of-the-year (0+) survival, is relatively constant over the months of May to
149 September we combined all available data into an annual mean for each stream reach
150 (Juanes *et al.* 2000). Quantitative electrofishing surveys (29% of samples) involved three
151 electrofishing runs per reach (approx. 50m) of river to yield a population estimate as
152 density of fish per m² of river based on catch-depletion. Semi-quantitative surveys (71%
153 of samples) involved just one run per site. Equations used to estimate equivalent
154 quantitative survey counts from semi-quantitative were established by regressing the third

fishing pass (Q) against the first fishing pass count (SQ) according to the methods outlined by Strange *et al.* (1989), by which the quantitative density of juvenile salmon = $2.13 + 1.41$ Semi-quantitative density ± 0.065 error (R-Sq = 82.5% 5.4standard error) while the quantitative density of juvenile trout = $0.703 + 1.35$ Semi-quantitative density ± 0.048 error (R-Sq = 88.6%).

The majority of rivers were electrofished once each year, but some were sampled more than once or had multiple sample sites. In these cases, a mean annual density was calculated for each reach (see Appendix 1 for the frequency of sampling within each river). Densities were log transformed to achieve normality and homogenise variances.

Electrofishing sites were matched to water chemistry samples based on their proximity, geology and stream order. Electrofishing reaches without comparable water chemistry data (n = 14) were excluded from any analysis of fisheries trends against chemical and climatic variables.

Water chemistry

Data on chemical quality, analysed by standard methods, were obtained from the Environment Agency Water Management Information System (WMIS) database (SCA, 1978, 1979, 1981, 1988). Ammoniacal nitrogen (mg/l), dissolved oxygen (mg/l), Biological Oxygen Demand (BOD [ATU]) (mg/l) and pH were monitored monthly throughout all years of the study except for 1993. The total concentration of ammonium salts (NH₄⁺) and free ammonia (NH₃) was determined from the reaction of ammonia

177 with hypochlorite to form monochloramine and measured colorimetrically at 656nm as a
178 blue indo-phenol complex using a Discrete Analyser - Aqua 800/Konelab 30
179 (SCA, 1981). Dissolved oxygen concentration was measured by the Winkler manual
180 titration method (SCA, 1979). The Biochemical Oxygen Demand (BOD) measured the
181 uptake of dissolved oxygen by a sample during 5 days at 20°C in the dark and was
182 analysed via a SKALAR automated system in the presence of allylthiourea (ATU) to
183 suppress the uptake of oxygen by ammonia (SCA, 1988). pH was measured
184 electrometrically with a glass electrode WTW530 pH meter (SCA, 1978).

185
186 Chemical samples were defined as either 'summer' (April - September) and 'winter'
187 (October - March), and mean calculated for the seasons antecedent to electrofishing.
188 Missing values were replaced, where possible, with the mean for the appropriate year,
189 season and river reach.

190

191 *Climatic variables*

192 Climatic data came from several sources. To assess climatic trends across the catchment
193 as a whole, mean monthly minimum (tmin), maximum (tmax) air temperatures (°C), and
194 rainfall (mm), were obtained from Ross-on-Wye (National Grid Reference (NGR) SO
195 597238; 51° 54' 40.55" N 2° 35' 8.92"), the meteorological station at which the most
196 complete daily records were available (Met Office, 2004). We supplemented these with
197 additional temperature records available from daily (1988-2004) or weekly (1982) data
198 from Llysdyman Field Centre, Newbridge-on-Wye (NGR SO 009 586; 53° 12' 59" N
199 3°27' 3" W), directly adjacent to the river temperature sites (see below). Fewer data were

200 available from stream or river temperatures, but extensive studies indicate that these can
201 be modelled as a reasonable approximation using air temperature: while local factors
202 such as groundwater inputs, evaporative cooling, shading and discharge affect the exact
203 nature of their inter-relationship, mean air and stream temperatures are closely correlated
204 over weekly to monthly time steps because both air and water are warmed by similar
205 processes (Webb, Clack and Walling 2003; Caissie 2006; Durance and Ormerod 2009).
206 As an example, between 1980 and 2003, monthly mean temperatures at Ross-on-Wye
207 explained 98% of the variation in mean monthly stream-water temperatures available
208 from the directly adjacent headwaters of the Afon Tywi with a regression slope of 0.81
209 (d.f.=294, F = 13,121, P<0.001 $r^2 = 0.97$; Durance and Ormerod 2007). This illustrated
210 that local stream temperatures tracked air temperature, but with increasing damping at
211 higher values. Calibrations between river temperature and air temperature at Llysdyman
212 available over a one-year period in 1982 at eight adjacent sites illustrated how this
213 damping effect varied between stream types, with unshaded higher-order tributaries of
214 the Wye tracking air temperature more directly than shaded low-order streams (Table 1;
215 Ormerod 1985; SO010512; SO014583; SN999569; SO033516; SN997530; SO019573;
216 SO032541; SO044487; altitudes 120-200m above sea level). We used these local
217 calibrations to estimate from the air-temperature series how stream temperature in
218 contrasting locations has varied through time. Temperatures for each salmonid sampling
219 location were further adjusted for altitude according to the environmental lapse rate of 6.5
220 °C per 1000 m.

222 Median winter (October -March) and summer (April - September) discharge (m^3/s) data
223 were taken from the Gwy and Hafren Flumes, operated by the Centre for Ecology and
224 Hydrology on Plynlimon, where the Wye rises ($52^\circ 27:26' \text{N}$, $3^\circ 47:46' \text{W}$). Our
225 assumption was that inter-annual trends in relative discharge here represented wider
226 regional pattern across the Wye even though the total [discharge-varied](#) between sites. We
227 validated this assumption by comparison with discharge at a gauged site on the Afon
228 Cothi, c 50km to the west in the adjacent Tywi catchment ($51^\circ 51:37' \text{N}$, $4^\circ 11:00' \text{W}$),
229 where discharge correlated highly significantly with the upper Wye ($r = 0.89$, $n = 289$
230 monthly mean values, $P < 0.0001$). Examination of other parameters to describe
231 discharge based on the flow-duration curve (e.g. 5% and 95% flow percentiles) gave
232 results that were highly inter-correlated with median discharge and equally inter-
233 correlated with variates describing inter-annual climate variability.
234
235 Because of expectations from patterns elsewhere in Wales (Durance and Ormerod 2007),
236 we investigated whether the North Atlantic Oscillation (NAO) contributed to inter-annual
237 variation in climate and temperature using [the mean difference between the normalised](#)
238 [sea level pressure over Gibraltar and the normalised sea level pressure over Southwest](#)
239 [Iceland. The NAO](#) index is associated with changes in the surface westerlies across the
240 North Atlantic to Europe and represents dry, cold winters when negative and warm wet
241 winters when positive (Hurrell, 1995). [Monthly](#) NOA index values between [1984 and](#)
242 [2004](#) were obtained from the Climatic Research Unit and used to calculate summer and
243 winter means for use in the principal components analyses described below (Climatic
244 Research Unit, 2005; Osborn, 2005).

245

246 *Data analysis*

247 To establish whether salmonid populations declined through time, the effect of year on

248 their respective density was established from multi-level linear regression (also called

249 mixed effects models) using the [lme function in R 2.9 \(R Development Core Team 2009\)](#).

250 Multilevel models are increasingly adopted over repeated measures ANOVA and time-

251 series analyses in longitudinal studies (Van Der Leeden,1998; Pinheiro and Bates 2000,

252 Twisk, 2006). Models account for the dependency of observations by recognising a

253 hierarchical structure in the data whereby observations are nested within rivers in this

254 instance. This enables analysis of continuous and relatively short time series data, [such as](#)

255 [our 19 year](#) salmonid population data. We used a two-level design, whereby observations

256 were clustered within rivers in a ‘random intercept’ model that accounted for the

257 autocorrelated nature of the repeated observations within rivers (Twisk, 2006). A random

258 intercept regression model that included a random slope improved the (log likelihood) fit

259 of the model (Twisk, 2006). The correlation between the random intercept and random

260 slope was used to indicate whether rivers with high or low densities of salmonids were

261 more or less susceptible to population decline. A negative correlation would indicate that

262 rivers with a higher density of salmonids had a low slope, or less dramatic decline

263 assuming a negative relationship between density and time.

264 Spearman’s correlation coefficients (r_s) were calculated between water quality, climate

265 and year. We then used Principal Components Analysis (PCA) separately on the

266 correlation matrices of climatic and water quality variables, respectively for summer and

267 winter, to derive variates describing trends in environmental variation through time.

To assess which synoptic environmental variates from PCA best explained trends in the density of juvenile salmonid populations through time, we again used multi-level linear regression. A two-level design, similar to that described for the assessment of the effects of time on density, was adopted whereby observations were clustered within rivers in a 'random intercept' model that accounted for the autocorrelated nature of the repeated observations within rivers (Twisk, 2006). The fixed effects of each of the climatic variables on salmonids density were therefore established after using random coefficients for each river to model the covariance structure of the data. The inclusion of a random slope into the random intercept regression model did not significantly improve fits. However, there was strong evidence to support the inclusion of a first-order autoregressive (AR1) term to model residual autocorrelation within rivers ($\Delta AIC = 8.0$ and 39.5 for salmon and trout respectively). The predicted change in density with each climatic variable was estimated by examining raw variables values at the 5, 25, 75 and 95 percentiles of PCA scores.

All data were transformed to reduce skew and kurtosis when appropriate. Analyses were repeated for juvenile salmon ($> 0+$) and juvenile trout ($> 0+$) and Bonferroni adjustment for multiple tests are reported (Quinn and Keough, 2002).

Results

Trends in salmonid density

Juvenile salmon and trout densities declined between 1985 and 2004 across the Wye catchment by 50% and 67%, respectively (Figure 2, Table 2). This change was

significant, as demonstrated by a negative regression coefficient for density of both salmon and trout juvenile with year (Table 2). The correlation between the random intercept and random slope was negative (salmon: -0.26, Wald Z =2.48; $p=0.013$; trout: -0.28, Wald Z =2.16; $p=0.031$) indicating that rivers with higher densities of salmonids had a low slope, or less dramatic decline in populations. In addition to declining trends through time, populations were characterised by marked inter-annual variations (Figure 2).

Long-term environmental change

From the early 1980s, water quality generally improved across the Wye catchment, seen for example in declining biochemical oxygen demand ('summer': $r_s = -0.59$ $P < 0.05$; 'winter' $r_s = -0.59$ $P < 0.05$) and ammonia ('summer': $r_s = -0.73$ $P < 0.01$; 'winter': $r_s = -0.39$ $P < 0.05$). Average concentrations of oxygen were seldom below 95% saturation, or below 9-10 mg/L, and did not decrease significantly through time despite increasing temperature (see below). These chemical variations were well captured by single principal components in either winter or summer (Table 3).

Mean air temperatures over the study area increased during the last 25 years by c 1.3 °C (from 8.5 to 9.8 °C), and local calibrations suggested that this would have increased river temperatures (Table 1; Figure 3). Thus, over the 19 years covered by data on salmonid density, headwaters were estimated to have warmed in summer, annually and in winter by 0.5, 0.6 and 0.7 °C, respectively, while larger tributaries warmed by 0.6, 0.8 and 1.0 °C. Estimated winter temperatures were strongly affected by the NAO in both headwaters

314 (annual mean winter temperature = 5.93 ± 0.15 °C + 0.212 ± 0.065 x NAO) and larger
315 tributaries (mean winter temperature = 6.40 ± 0.19 °C + 0.279 ± 0.086 x NAO), with both
316 relationships highly significant ($F_{1,24} = 10.40$, $r^2 = 0.27$, $P < 0.01$). After accounting for
317 this effect, winter warming over the 19 years of the salmonid study was 1.1 and 1.4 °C in
318 headwaters and larger tributaries, respectively (Figure 3).

319

320 In contrast to temperature, discharge in the Wye has not changed directionally through
321 time over the period studied, but low and high flow periods have been apparent (Figure
322 4). Nor have rainfall or insolation (as daily hours sun) changed through time (both $r_s <$
323 0.3 , $P > 0.1$). Inter-annual variations in all these climatic variables were well described in
324 PCA by single variates. Among summers, positive scores in this component reflected
325 low discharge, high maximum temperatures and sunshine while negative values reflected
326 increased rainfall and discharge when negative (Table 3). In winter, climatic variations
327 mostly reflected warmer temperatures, higher rainfall, greater discharge and a stronger
328 contribution from the NAO than in summer (Table 3).

329

330 *Environmental correlates with salmonid density*

331

332 Individual Spearman's correlations showed that brown trout populations declined
333 significantly with increasing maximum temperature ($r_s = -0.25$, $P=0.02$) and discharge (r_s
334 $= 0.12$ $P=0.02$), while salmon densities declined with increasing solar radiation ($r_s = -0.17$
335 $P=0.002$) and maximum temperature ($r_s = -0.126$ $P=0.018$). However, these individual
336 relationships were weak, and multilevel regression produced stronger relationships with

the synoptic climate variates in both species, particularly when lagged against the previous summer (Table 4). Densities of both Atlantic salmon and brown trout declined with increasing scores on the index of antecedent summer climate (i.e. climate PC1), indicating that reductions in density were greatest following hotter, sunnier and drier conditions (Table 4; Figure 5). On average, a shift across the inter-quartile range for this variate equated to a 0.3 °C increase in maximum temperature and a 10.1 mm decrease in monthly rainfall. This, in turn, appeared to reduce salmon densities by 1.7 salmon per 100m² of river and 1.8 trout (per 100m² of river) respectively (Table 5), or around 17-20% of typical mean densities at the beginning of the study. Neither winter climate nor variates describing water quality explained significant variations in salmonid density.

Discussion

These data, collected over a 20-year period from two salmonids with contrasting life-cycles, support all three of our hypotheses: both species have declined substantially and unequivocally across the Wye catchment, with trends and fluctuations better explained by climatic factors than any other variable examined. Of considerable importance, changes in both migratory Atlantic salmon and non-migratory brown trout populations appeared to be linked to synoptic climatic effects, with both species' populations declining when increasing summer temperature was combined with reduced discharge. While factors at other scales might affect salmon population and demographics, such as at-sea survival or exploitation through commercial fishing (e.g. Gee and Milner, 1980; Finney *et al.*, 2000; McFarlane *et al.*, 2000; Quinn *et al.*, 2006; Ruggerone *et al.*, 2007), within-catchment processes affecting recruitment or survival must also be important (Rieman *et al.*, 2001;

360 Regetz, 2003). Local water-quality effects in the Wye system include pollutants such as
361 pyrethroids (Moore and Waring, 2001), episodic acidification in the upper catchment
362 (Lewis et al. 2007) and eutrophication in the lower catchment (Clews and Ormerod
363 2009), but these effects have all abated through time and so cannot explain population
364 reduction (Ormerod and Durance 2009). Notwithstanding the important caveat that our
365 analysis is based on correlation, climatic effects are the most plausible explanation for the
366 trends and fluctuations observed, as well as the best statistical explanation. A reduction
367 in commercial net fisheries in UK and Ireland over the study period also supports this
368 assertion. We note here that, although effects on both brown trout and salmon in our
369 analysis were apparently captured by the same broad climatic variables, the exact
370 processes involved could differ between these two species, not least because of their
371 different habitat requirements within stream systems (Armstrong et al., 2003).

372
373 One important factor to consider in assessing long-term population data under varying
374 climatic conditions is that temperature can affect the efficiency of electrofishing gear.
375 Such effects could, in turn, potentially confound any putative effects of increasing
376 temperature on population estimates. However, the effects of a 1°C temperature increase
377 on capture efficiency are likely to be far smaller than the declines observed both salmon
378 (50%) and trout juveniles (67%) in this study: the conductivity of stream water is reduced
379 by only 2% per °C (Bohlin *et al.* 1989). Alabaster and Hartley (1962) described the
380 impact of conductivity on the percentage of a fish population caught by direct current
381 electrofishing according to the regression equation $y = 0.27x - 9.6$, where y is the
382 percentage catch, and x is the conductivity ($\mu\text{S cm}^{-1}$) of the water. In 2003, the *in situ*

conductivity was measured across streams within the Wye catchment and ranged from 161 to 352 $\mu\text{S cm}^{-1}$. According to Alabaster and Hartley's (1962) equation, an increase in temperature of 1°C would increase the percentage of the fish population caught, rather than decreasing it, but by just 0.9 to 1.9 % over the range of conductivities encountered in the Wye. In addition to altering the stream conductivity, temperature can also affect fish behaviour and physiology (Bohlin *et al.* 1989). At higher water temperatures, fish are more likely to avoid sampling gear due to an increased metabolism and associated capacity for movement (Hayes and Baird 1994). Conversely, behaviours such as fish burrowing into the substrate at low temperatures may also prevent capture, and floatation rates are greater in warmer water thus possibly offsetting the effects of the former (Reynolds, 1996; Roni and Fayram 2000). These effects are currently harder to estimate quantitatively than temperature effects through altered conductivity.

In locations elsewhere, there is strong evidence that climate is a key factor regulating salmonid populations (Beamish *et al.*, 1999; Beaugrand and Reid, 2003; Tolimieri and Levin, 2004; Zabel *et al.*, 2006; Walsh and Kilsby, 2007). Climatic effects on salmonids, such as those we detected, are therefore entirely consistent with expectation from current climatic trends, to which temperate, upland rivers appear highly sensitive (Durance and Ormerod 2007; 2009). Climate-related variables, such as rainfall and temperature, can impact directly on the habitats preferred by salmonids, influencing their behaviour, growth and survival (e.g. Flebbe *et al.*, 2006; Seo *et al.*, 2006; Taylor 2008). Placed by classical studies of river zonation into the narrow, shallow, fast flowing, clear water, upstream 'trout zone' (Hawkes, 1975), the fry (0+) and juveniles (<0+) of *S. salar* and *S.*

406 *trutta* require well-oxygenated ($5.0\text{--}5.5\text{ mg l}^{-1}$), cool (optimally $13\text{--}16\text{ }^{\circ}\text{C}$), relatively fast
407 flowing water (approximately $10\text{--}30\text{ cm s}^{-1}$ and $20\text{--}50\text{ cm s}^{-1}$ respectively), and
408 inhabiting deeper water as they grow (Armstrong *et al.*, 2003). Conditions in the Wye,
409 particularly in larger unshaded tributaries, have increasingly exceeded this temperature
410 optimum over the last 20 years (see Figure 3). As poikilotherms, the foraging behaviour
411 and habitat use of salmonids is strongly influenced by temperature (Armstrong *et al.*,
412 2003). Elevated temperatures in temperate climates may extend the growing season for
413 salmonids while also increasing metabolic demands and food requirements while
414 possibly also increasing susceptibility to disease (Elliot *et al.*, 1998). For example, in
415 alpine streams in Switzerland increased water temperatures induced higher incidences of
416 proliferative kidney disease in brown trout at higher altitudes (Hari *et al.*, 2006).

417

418 Changes in the intensity and frequency of rainfall affect river-flow regimes and have
419 implications for the accessibility, permanence and suitability of habitats, and hence
420 salmonid distribution (Armstrong *et al.*, 2003; Hakala and Hartman, 2004). Recent
421 experimental manipulations of flow to mimic low summer discharge in a British chalk
422 stream produced results consistent with our data from the Wye, showing how increased
423 mortality of both salmon and trout under low summer flow reflected reduction in habitat
424 availability (Riley, *et al.*, 2009). Interesting in our study was that low-flow and warming
425 effects both appeared to contribute to population reduction, and again this is consistent
426 with previous observation. For example, in the Upper Rhône River, low flow and high
427 temperature favoured thermophilic fish species (e.g. *Leuciscus cephalus* and *Barbus*
428 *barbus*) at the expense of northern, cold-water fish species (e.g. *Leuciscus leuciscus*)

(Daufresne *et al.*, 2004). One possibility that requires further investigation is that the availability of thermal refuges in rivers declines at low flow in ways that prevent salmonids from finding and occupying locally cooler micro-environments (Clark, Webb and Ladle 1999; Arscott, Tockner and Ward 2001; Breau *et al.* 2007). The risk of such effects is supported by evidence that i).small-scale thermal gradients increase in rivers with increasing depth (as well as with lateral shade; Clark *et al.* (1999) and ii) increased discharge and depth increase thermal mass and thermal inertia such that rivers track air temperature less closely as flow increases (Webb *et al.* 2003). Further work is now required to establish exactly where in river systems, when and how combined low flows and elevated temperatures might be most damaging to salmonids.

One technical component of our analytical approach is that it appears to assume linear responses between salmon, trout and environmental processes affecting populations. However, species do not necessarily respond linearly to environmental gradients (Armstrong *et al.*, 2003).. For example, growth rates are temperature-dependent and reach an asymptotic optima at 15.9 and 13.1 °C in salmon and trout respectively (Elliott and Hurley, 1995, 1997). To assess the possibility of non-linear relationships between climate and salmon or trout densities, we re-fitted models using generalised additive mixed modelling using the GAMM approach of Wood (2006) *Generalized Additive Models*, Chapman & Hall) – i.e. employing generalised cross validation to select an appropriate degree of smoothing for each variable. There was insufficient evidence that the relationships between salmon, trout and summer climate or any measure of water quality were non-linear, selecting a linear fit for the model. The linear models presented

here therefore provide the best current guide to the potential responses of salmonids to climatic variation within their optimal range. Interestingly, there was some evidence of a weak non-linear relationship between trout, salmon and winter climate, but it arose only with lags of > 1-2 winters before the time of sampling, and moreover was not statistically significant after modelling residual autocorrelation. We therefore suggest that such winter climatic effects in the Wye, either alone or in combination with summer effects, would warrant further investigation only when a longer data run is available. Salmonid life cycles operate over multiple years and are complex, involving migration to accommodate the different habitat preferences of each life-stage (see Crisp, 1996; Armstrong *et al.*, 2003). For example, the life cycle of salmon in the Wye system require at least 2 years from egg to adult spawner, and more in the case of multi-sea-winter fish (>3 years) which made up approximately 90% of rod catches in 1977 (Edwards and Brooker, 1982). Climatic effects operating on salmonids are therefore integrated across the entire lifespan of the fish as well as that of the previous generation. The numbers of Atlantic Salmon spawners returning to the Wye have declined over the study period – notably for the number and proportion of multi-sea-winter fish (Environment Agency, 2003a). At least in this species (as opposed to the Wye's brown trout), the influence of climatic and anthropogenic factors affecting potential spawners in the marine environment cannot be discounted as an influence on the decline of salmon juveniles (Kennedy and Crozier 1993; Potter *et al.*, 2003; Jonsson and Jonsson, 2004). Notwithstanding these possibilities, the period between emergence and the establishment of feeding territories in salmonids is critical, and this is the period we were particularly interested in capturing when testing hypotheses about summer climate (Armstrong *et al.*, 2003; Nislow *et al.*,

2004). Climatic variables presented here operated over this critical period in the development of the juvenile salmonids in the Wye. Correlations between climatic variables and salmon densities were generally greater for the preceding year when considered against the each of the preceding 7 years respectively. The relatively short time-lags over which climate variables were found to affect salmon density significantly imply that freshwater condition rather than marine factors affected the variations observed in juveniles.

Future climatic effects and their management

If the effects detected in the Wye are substantiated by surveys or experiments elsewhere, there are clearly potential implications for the future status of salmonids under climate change. This has particular importance in the case of Atlantic salmon given its position on the EU Habitats Directive (92/43/EEC) and its relevance to the designation of rivers as ‘Special Areas of Conservation as part of the ‘Natura 2000’ network. The UK climate is likely to warm between 2-5 °C by 2080 (Hulme *et al.*, 2002), with winters in western Britain wetter but summers drier (Conway, 1998; Hulme *et al.*, 2002). Effects of this magnitude are already developing in British rivers (Durance and Ormerod 2007; 2009), while studies in the Upper Wye suggest that the occurrence and amount of precipitation will decrease in summer and autumn, while evapotranspiration will increase, resulting in more frequent ‘low flows’ (Pilling and Jones, 2002). Extreme drought events, as experienced in 1990, 1995, 2003 and also in 1976 with catastrophic effects on salmonids (Edwards and Brooker, 1982), are likely to occur at increased frequency. Given the trends recorded here, changes of this type would be detrimental to salmonid populations unless

498 adaptive management actions are taken to offset the worst effects. Maintaining river
499 discharge through reducing abstraction and increasing compensation flow will be
500 important, while the use of riparian shade to reduce the effects of adverse summer
501 temperatures is also gaining favour (Rutherford *et al.*, 2004; Watanabe *et al.*, 2005;
502 Ormerod 2009). Our own evidence supports this effect (Figure 3), while similar results
503 elsewhere suggests that riparian shade can reduce summer temperature at least as
504 effectively as the effect of groundwater damping on chalk-fed rivers (Table 6). On this
505 basis, riparian shading could become a critical tool in maintaining salmonids in the
506 southern part of their current European range.

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For Review Only

Table 1: Generalised regression relationships ($y = a + bx$) between weekly mean stream temperature at sites in the catchment of the Welsh River Wye and air temperature at Newbridge-on Wye (After Ormerod 1985). Regressions are shown respectively for lower-order headwaters with riparian shading and larger-order main channels with less riparian vegetation.

	$a \pm 95\% \text{ CI}$	$b \pm 95\% \text{ CI}$	N	$100.r^2$
Headwaters	3.40 ± 0.40	0.715 ± 0.039	159	89.1
Main channels	3.07 ± 0.77	0.942 ± 0.075	77	89.3

Table 2. Multilevel regression models of log transformed juvenile density of a) salmon and b) trout against year in the River Wye catchment detailing regression coefficients (Estimate ± SE), 95% confidence intervals (CI) and corresponding p-values.

a) Salmon				
Variable	Estimate (SE)	t	p	95% CI
Intercept	34.08 (4.83)	7.06	<0.001	24.31-43.84
Year	-0.02 (0.002)	-6.93	<0.001	-0.02 - -0.01
b) Trout				
Variable	Estimate (SE)	t	p	95% CI
Intercept	28.59 (5.4)	5.30	<0.001	17.67-39.50
Year	-0.01 (0.003)	-5.16	<0.001	-0.02- -0.01

Table 3. Principal Component (PC) axes representing variation in ‘climatic variables’ and ‘water quality’ relevant to the Wye system recorded between 1985 and 2000 in summer (April - September) and winter (October - March), respectively. Eigenvectors indicate the loading of variables on the first PC axis extracted in Principal Component Analyses.

Summer ‘climate’ component		Summer ‘water quality’ component	
48.9 % variance explained		40.3 % variance explained	
Sun hours	0.907	Ammonia N mg/l	0.722
Discharge m ³ /s	-0.856	BOD mg/l	0.762
Rain mm	-0.851	Dissolved Oxygen mg/l	-0.639
Tmin °C	0.081	pH	0.317
Tmax °C	0.755		
NAO index	0.278		
Winter ‘climate’ component		Winter ‘water quality’ component	
45.0 % variance explained		47.3 % variance explained	
Sun hours	0.278	Ammonia N mg/l	0.739
Discharge m ³ /s	0.702	BOD mg/l	0.606
Rain mm	0.619	Dissolved Oxygen mg/l	-0.696
Tmin °C	0.857	pH	0.704
Tmax °C	0.885		
NAO index	0.479		

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Table 4. Multilevel regression models of environmental factors on log transformed juvenile density in a) salmon and b) trout in the River Wye catchment detailing regression coefficients (Estimate $\pm$ SE), 95% confidence intervals (CI) and corresponding p -values.

a)

Variable	Estimate (SE)	t	p	95% CI
Intercept	0.67 (0.04)	16.85	<0.001	0.59 - 0.74
Summer 'climate' last year	-0.04 (0.01)	-2.98	0.003	-0.06 - -0.01
Winter 'climate' last year	-0.01 (0.01)	-0.45	0.654	-0.03 - 0.02
Summer 'water quality' last year	-0.03 (0.02)	-1.34	0.180	-0.07 - 0.01
Winter 'water quality' last year	-0.02 (0.02)	-0.68	0.500	-0.06 - 0.03

b)

Variable	Estimate (SE)	t	P	95% CI
Intercept	0.69 (0.04)	17.32	<0.001	0.61 - 0.76
Summer 'climate' last year	-0.06 (0.01)	-4.82	<0.001	-0.08 - -0.03
Winter 'climate' last year	-0.02 (0.01)	-1.37	0.173	-0.01 - 0.04
Summer 'water quality' last year	-0.04 (0.02)	-1.91	0.056	-0.08 - 0.00
Winter 'water quality' last year	0.03 (0.02)	1.17	0.243	-0.02 - 0.07

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828 **Table 5.** Values of raw climatic variables (monthly average) at 5, 25, 75 and 95
829 percentiles of Principal Component scores derived from a Principal Component Analysis
830 of summer climatic variables relevant to the Wye river system (see Table 3 for loadings).

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Percentiles	PC1summer scores	Rainfall (mm)	Sun (hours)	NAO	Discharge (m ³ / s)	Tmax °C	Tmin °C
5%	-1.469	62.4	173.3	-0.131	0.346	18.2	9.3
25%	-0.828	48.2	169.8	-0.588	0.264	18.6	10.1
75%	0.761	38.2	202.1	-0.222	0.130	18.9	9.0
95%	1.762	36.0	213.6	0.340	0.124	20.5	10.0

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Table 6. Slopes relating monthly mean or median stream to air temperature in a range of lowland chalk-fed streams and Welsh rivers and streams (1: Durance and Ormerod 2009; 2: Mackey and Berrie 1991; 3: Durance and Ormerod 2007; 4: Crisp 1997; 5: this study)

Site	$b \pm SE$
<i>Chalk streams</i>	
Itchen, Eastleigh ¹ (SU 454157)	0.76 ± 0.01
Bere, Dorset ¹ (SY 859 919)	0.68 ± 0.02
Avon, Amesbury ¹ (SU 151 413)	0.51 ± 0.02
Frome ² (SY868861)	0.94 ± 0.02
Lambourne ² (SU452693)	0.62 ± 0.02
Winterbourne ² (SU453694)	0.48 ± 0.02
Tadnol Brook ² (SY800874)	0.74 ± 0.03
<i>Welsh rivers and streams</i>	
Moorland stream (CI6; SN772 556) ³	0.94 ± 0.04
Moorland/forest stream (AT; SN804 538) ³	0.97 ± 0.04
Forest stream (LI1; SN809 529) ³	0.78 ± 0.09
Plynlimon forest stream (Hafren; SN8487) ⁴	0.66-0.73
Plynlimon forest stream (Hore; SN8388) ⁴	0.51-0.71
Wye catchment, wooded headwaters ⁵	0.72 ± 0.04
Wye catchment, main tributaries ⁵	0.94 ± 0.07

Figure Legends

Figure 1. Location of electrofishing sites within the catchment of the Welsh River Wye (small symbols), showing also those with chemical data (larger symbols).

Figure 2. Standardised (mean z scores $\pm$ SE) relative densities of juvenile (>0+) salmon and trout juveniles averaged across tributaries of the Welsh River Wye, 1985 – 2004. N indicates the number of rivers contributing to mean annual density in each year.

Figure 3. Long-term trends the annual (a: $y = 0.0413x - 70.759$ ●; $y = 0.0314x - 52.637$ ○; $r^2 = 0.38$), summer (b; $y = 0.0339x - 50.414$ ●; $y = 0.0257x - 37.194$ ○; $r^2 = 0.1164$) and winter (c; $y = 0.0504x - 93.782$ ●; $y = 0.0383x - 70.113$ ○; $r^2 = 0.1411$) temperature of tributaries of the River Wye as estimated from trends in air temperature using generalised calibrations respectively from three larger, unshaded tributaries (●) and five shaded headwaters (○). Panel d) shows trends in residual winter temperature after accounting for the significant of the NAO (see text) ($y = 0.0732x - 145.95$ ●; $y = 0.0556x - 110.78$ ○; $r^2 = 0.4264$).

Figure 4. Long-term variations in discharge during summer (a) and winter (b) at the CEH Hafren Flume, Plynlimon.

Figure 5. Densities of >0+ salmon (a) and brown trout (b) per 100m² reach averaged (mean $\pm$ SE) across tributaries of the Wye catchment in each year plotted against an index on antecedent summer climate. This is derived as the first component from a Principal Components Analysis (PC) on climatic variables during the (see Table 3).

Appendix 1. Frequency of sampling of salmonids in the Wye catchment 1985-2004. Years which included quantitative sampling of rivers are indicated by *. Monitoring was not undertaken in 1996. Rivers which were split into upstream and downstream reaches according to proximity, geology and stream order are indicated by upstream ‘u/s’ and downstream ‘d/s’, respectively.

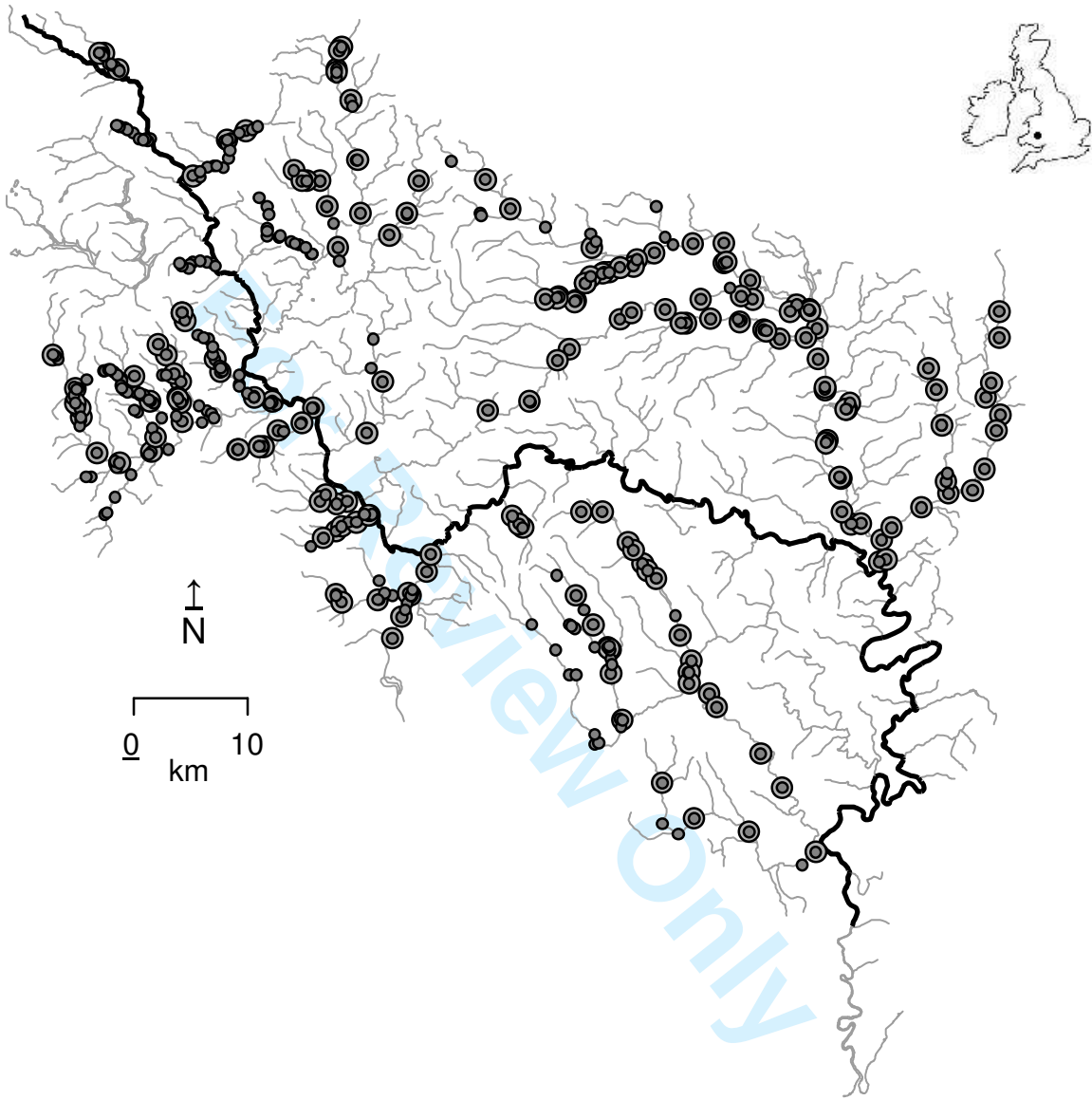
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River	Year																	
	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1997	1998	1999	2000	2002	2003	2004
Aran	2*	2	1	1	1	1	1	1	1	1	1	3	0	3	0	1*	3*	1*
Arrow (d/s)	2	2	1*	1	0	0	0	0	0	0	0	1	4*	1	0	1*	2*	1*
Arrow (u/s)	4	4	3*	3	4*	4*	4*	3*	4*	3*	3	6	2*	6	0	2*	6*	2*
Bidno	2	2	2	2	2	2	2	2	8*	2	1	2*	1*	2*	1*	1*	5*	1*
Bleddfa	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0*	2*	0*
Cammarch	1	1	0	0	1	1	2	2	2	2	2	3	0	3	0	1	4	1
Chwerfri	3*	2*	2*	2*	2	4	1	1*	17*	1	2	3	0	2	0	1*	9*	1*
Cledan	2	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	2	0
Clettwr	0	0	0	0	0	0	0	0	0	0	0	4	3	3	0	0	2	0
Clywedog	3*	2*	2*	2*	2*	2*	2*	1*	1*	2*	2	6*	3*	2*	1*	1*	5*	1*
Cnyffiad	2	1	1	1	1	1	1	1	14*	1	1	3	3	0	0	0	2	1
Dernol	2*	2*	1*	1*	1*	1*	1*	1	9*	1*	1	1*	1*	1*	1*	1*	3*	1*
Dore	3	6	3*	3*	3*	3	3*	5*	3*	1*	2	4	6*	4	0	0	1	0
Duhonw	2*	2*	1*	1*	1*	1*	2*	3*	2*	2*	1	5*	6*	1*	1*	0	6*	1*
Dulas (Ithon)	2	2	1	1	0	1	1	0	11*	0	1	2*	0	2	1*	1*	2	1*
Dulas brook	0	0	0	0	0	0	0	0	0	0	0	3*	3*	0	0	0	2	0
Edw	4*	3*	2*	2*	2*	2*	2*	2*	2*	2*	2	2*	1*	2*	1*	1*	4*	1*
Einon	1	1	0	0	0	0	0	1	1	1	1	1	0	1	0	1*	1*	1*
Frome	0	0	0	0	1	1	3	5	3	0	3	5	0	6	0	0	2	0
Garth Dulas	3	3*	2*	2*	2*	2*	1*	2*	2*	2*	2	4*	8*	7*	0	1*	5*	1*
Gwesyn	1	1	1	0	1	1	1	1	1	1	1	1	0	2	0	0	1	0
Hafrena	0	0	0	0	0	0	0	0	0	0	0	3*	3	0	0	0	1	0
Hindwell	2	2	1*	1*	2*	2*	2*	0	2*	1*	2	9*	9	0	0	1*	1*	1*
Honddu	3	7	4*	4*	4*	4*	4*	3*	3*	3*	3	4	0	4	0	0	2	0
Irfon	5*	5*	4*	3	4*	4	2	2	12*	2	2	1	0	6	0	2*	4*	1*
Ithon	5*	4*	2*	2*	2*	2*	2*	2*	2*	1	3	6*	1*	4*	1*	2*	4*	2*
Lingen Brook	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	2	0
Llanwrthwl Brook	2*	1*	1*	1*	1*	1*	1*	1	10*	1*	0	1*	1*	1*	1*	1*	1*	1*
Llynfi	4*	3*	2*	2*	2*	2*	2*	4*	2	0	2	3	0	3	0	2*	5*	1*
Llynfi dulas	2	1	0	0	0	0	0	0	0	0	0	4	2	2	0	0	4	0
Lodon	0	0	0	0	0	0	2	3	2	0	2	2	0	1	0	1*	4*	1*
Lugg (d/s)	1	1	1*	1	0	1	0	8	0	1	1	2	11*	2	0	0	0	4*
Lugg (u/s)	6	5	2*	2*	5*	3*	3*	4*	4*	4*	4	5	0	5	0	2*	7*	2*
Marteg	4*	3*	2*	2*	2	2	2	2	17*	2	2	3*	1*	3*	1*	2*	8*	2*
Monnow	3	7	3*	3*	3*	3*	3*	2*	3*	2*	2	4	5*	4	3*	4*	9*	0
Nant Gwynfel	0	0	0	0	0	0	1	1	0	1	1	1	1	1	0	0	1	0
Norton Brook	1	1	1	1	0	0	1	1	1	1	0	1	0	1	0	0	2	0
Olchon	1	3	0	1	1	1	1	1	1	0	1	1	0	1	4*	4*	8*	0
Pinsley Brook	2	2	1	0	1	1	1	1*	1	1	0	1	0	4	0	2*	4*	2*
Sgithwen	2*	2*	1*	1*	1	1	0	0	0	0	0	6*	6	6	0	2*	4*	1*
South Dulas	4*	2*	2*	2*	1*	1*	2*	1	2*	2*	2	2*	1*	2*	1*	1*	3*	2*
Triffrwyd	2	1	1	1	1	1	1	1	1	0	1	1	0	1	0	0	2	0
Trothy	3	5	2	2	2	2	2	1	4	0	2	4	0	3	0	0	0	0

Figure 1



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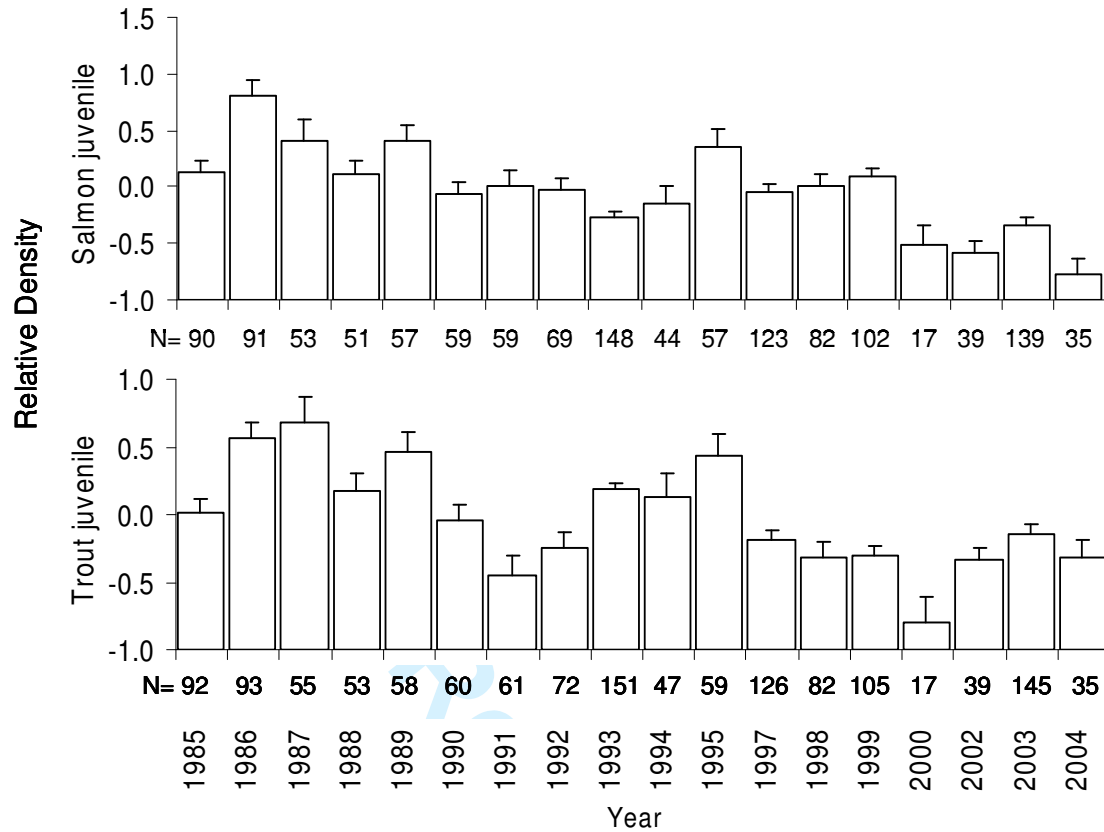


Figure 2

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Figure 3:

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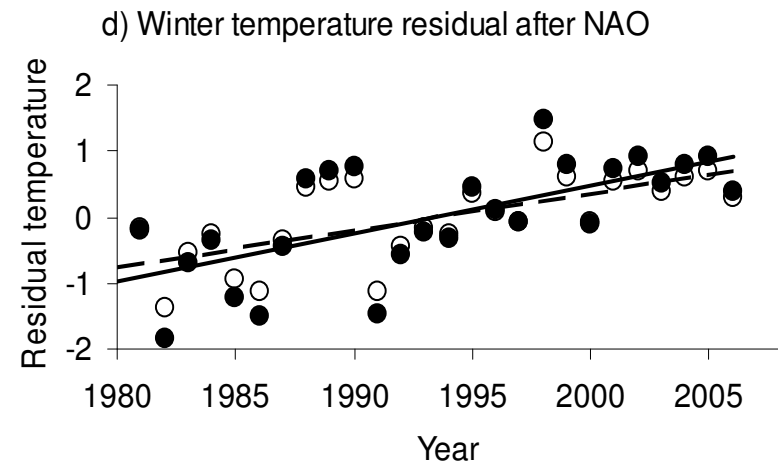
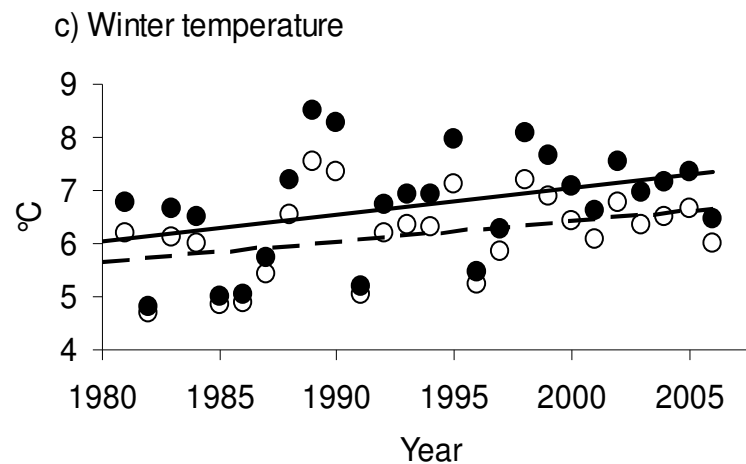
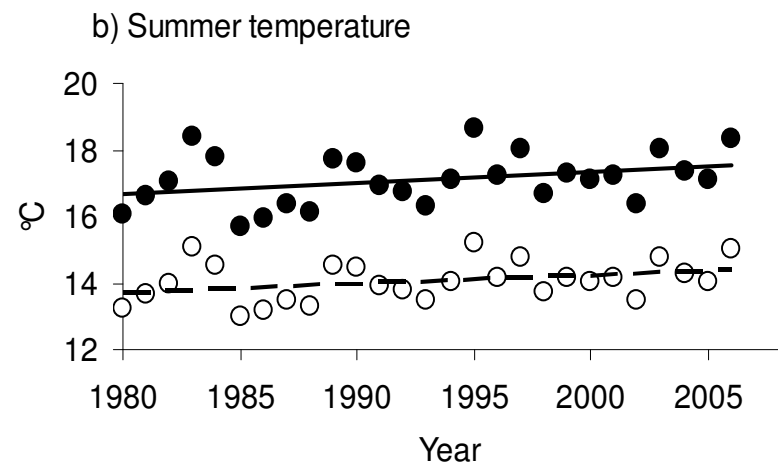
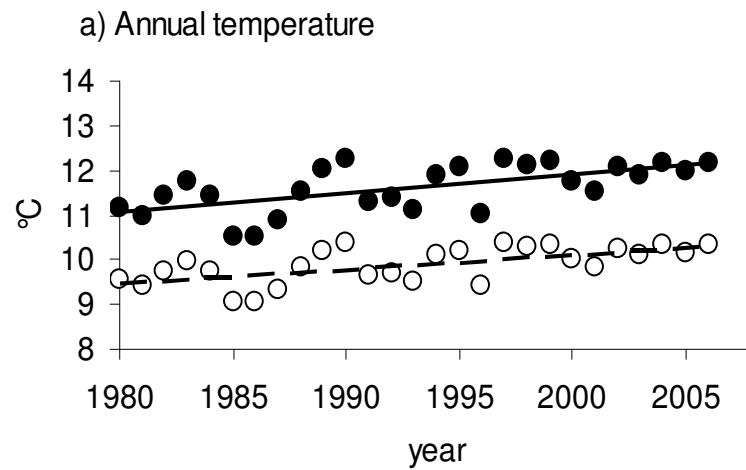


Figure 4

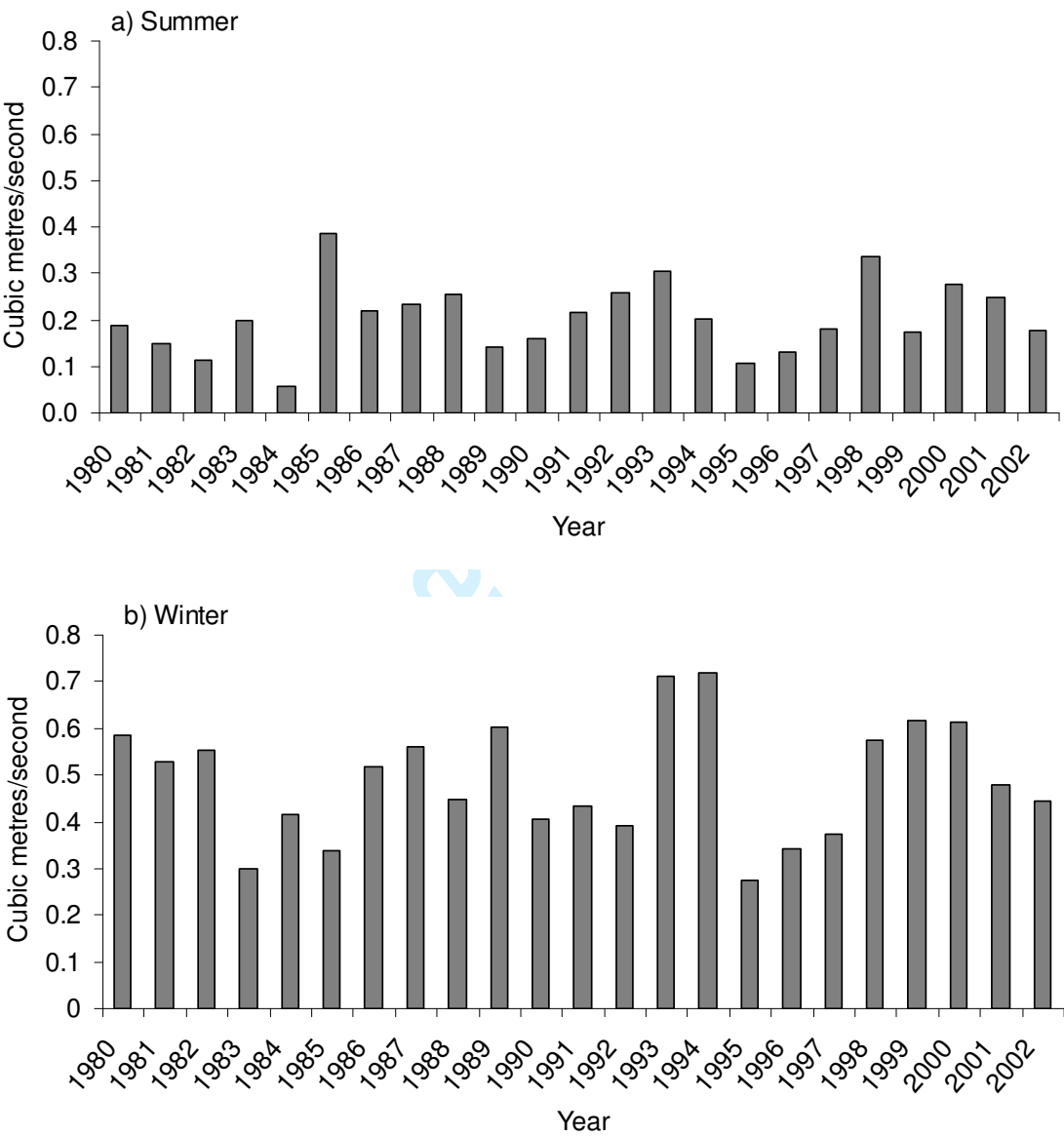


Figure 5

