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

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Keywords:	Climate , discharge , long-term study, river, salmon, stream, temperature, trout.
Abstract:	<p>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.</p> <p>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.</p> <p>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.</p>

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	<p>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</p>



For Review Only

1 **Juvenile salmonid populations in a temperate river system** 2 **track synoptic trends in climate**

3
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9
10 **Running head:** *Climate and salmonids*

11 12 **Abstract**

13
14 Widespread decline among Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*)
15 over recent decades have been linked to pollution, exploitation and catchment
16 modification, but climate change is increasingly implicated. We used long-term,
17 geographically extensive data from the Welsh River Wye, formerly a major salmon river,
18 to examine whether climatically-mediated effects on juveniles (> 0+) might contribute to
19 population change.

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

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

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

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

39
40 *Keywords:* Climate, discharge, long-term study, river, salmon, stream, temperature, trout.

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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*
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*
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*

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4 65 *al.*, 2006). Commercial fishing of Atlantic salmon has occurred extensively across near-
5
6 66 shore areas of Europe, including Ireland and the UK, and mortality from fishing has
7
8 67 previously been implicated in decline (Common Fisheries Policy, Council Regulation
9
10 68 2371/2002/EC; Potter, *et al.*, 2003). Evidence from angling catches suggests that
11
12 69 salmonid populations in rivers have not always recovered followed the reduction and
13
14 70 closure of commercial net fisheries in the UK over the last two decades, although this is
15
16 71 likely confounded by declining angler participation (Arahamian *et al.* 2009).

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21 72 Speculation is now growing that the reduction of salmonid populations across regions
22
23 73 must involve even broader-scale pressures than those outlined above, and climatic
24
25 74 variations are implicated increasingly. Climate affects salmonids through precipitation
26
27 75 and water temperature, with consequences for growth, development, behaviour and
28
29 76 survival both in freshwater and marine stages (e.g. Flebbe *et al.*, 2006; Seo *et al.*, 2006;
30
31 77 Walsh and Kilsby 2007; Taylor 2008). In addition, reductions in flow can reduce the
32
33 78 accessibility of habitats and affect species' survival and distributions (Armstrong *et al.*,
34
35 79 2003; Hakala and Hartman, 2004; Riley, *et al.*, 2009). Similarly, increased stream
36
37 80 temperatures may restrict the availability of thermal refugia in these typically cool-water
38
39 81 fishes (Eaton *et al.* 1995; Breau, *et al.*, 2007). At sea, rising sea-surface temperature is a
40
41 82 factor in population change (Beamish *et al.*, 1999; Beaugrand and Reid, 2003; Tolimieri
42
43 83 and Levin, 2004; Todd *et al.* 2008). While much attention has focused on directional
44
45 84 climate change the North Atlantic Oscillation (NAO) is also linked to changes in fish
46
47 85 production and ecology in both marine and freshwater ecosystems (Elliott *et al.* 2000;
48
49 86 Bradley and Ormerod, 2001; Parsons and Lear, 2001). Inter-annual variations in climate
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87 – for example through drought – can also have large effects on salmonids (Elliott *et al.*
88 1997)

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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).

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3 109 Here, we identify large-scale environmental correlates with trends and **fluctuations** in the
4
5 110 density of Atlantic salmon and brown trout across the Wye system over a 20-year period
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7
8 111 from 1984. Specifically, we test the hypotheses that i) densities of juvenile brown trout
9
10 112 and Atlantic salmon have declined across the Wye catchment and ii) trends are better
11
12 113 explained by climatic factors, rather than local water quality and iii) migratory Atlantic
13
14 114 salmon are equally tied to climatic effects as are brown trout, which might be expected if
15
16 115 climatic effects on freshwaters are important in salmonid trends.
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22 117 **Study Area**

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26
27 119 The River Wye, in temperate western Britain, rises at 677m OD (52° 28' N, 3° 45' W)
28
29 120 before flowing south eastwards to join the Severn Estuary (Figure 1). Typical of upland,
30
31 121 high-velocity rivers in the UK, the Wye dominantly drains a mix of rough grazing,
32
33 122 pastoral agriculture, and deciduous woodland or forest plantation, while arable farming
34
35 123 predominates in the lower Wye valley (Edwards and Brooker, 1982). The general
36
37 124 ecology, land use and water quality have been described extensively (Edwards and
38
39 125 Brooker, 1982; Ormerod and Edwards, 1987; Jarvie *et al.* 2003; Clews and Ormerod,
40
41 126 2009). The temperate climate means that precipitation averages around 912mm per
42
43 127 annum across the catchment, although the precipitation volumes increase towards the
44
45 128 north and west (Hughes and Morley, 2000) to 2500mm per annum (Jarvie *et al.*, 2003;
46
47 129 NERC, 2005). Typical annual mean temperatures range from 8-11 °C, and the highest
48
49 130 monthly means reach c 19 °C.
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3 132 Partly because of its importance for Atlantic salmon the Wye river system is both a Site
4
5 133 of Special Scientific Interest (SSSI) and Special Area of Conservation (SAC) under the
6
7 134 EU Habitats Directive (Directive 92/43/EEC) (Joint Nature Conservancy Committee,
8
9 135 2004).

136 **Materials and Methods**137 *Overall study design*

17 138 Trends in salmonid populations between 1985 and 2004 were assessed from 41 of the
18
19 139 Wye's tributaries, while hydrochemical and climatic correlates with fish density were
20
21 140 appraised on 27 tributaries from which chemical data were available. Fish population data
22
23 141 were used to investigate trends in salmonid populations through time and also to whether
24
25 142 trends were catchment-wide.
26
27

143144 *Salmonid data*

34 145 Juvenile salmonid data were derived by electrofishing by the Environment Agency,
35
36 146 Wales (Environment Agency and CEFAS, 2004) during summer (April to October) most
37
38 147 frequently in August (61% of samples). Since post young-of-the-year (> 0+) survival,
39
40 148 unlike young-of-the-year (0+) survival, is relatively constant over the months of May to
41
42 149 September we combined all available data into an annual mean for each stream reach
43
44 150 (Juanes *et al.* 2000). Quantitative electrofishing surveys (29% of samples) involved three
45
46 151 electrofishing runs per reach (approx. 50m) of river to yield a population estimate as
47
48 152 density of fish per m² of river based on catch-depletion. Semi-quantitative surveys (71%
49
50 153 of samples) involved just one run per site. Equations used to estimate equivalent
51
52 154 quantitative survey counts from semi-quantitative were established by regressing the third
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3 155 fishing pass (Q) against the first fishing pass count (SQ) according to the methods
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5 156 outlined by Strange *et al.* (1989), by which the quantitative density of juvenile salmon =
6
7 157 $2.13 + 1.41$ Semi-quantitative density ± 0.065 error (R-Sq = 82.5% 5.4standard error)
8
9
10 158 while the quantitative density of juvenile trout = $0.703 + 1.35$ Semi-quantitative density \pm
11
12 159 0.048 error (R-Sq = 88.6%).

13
14 160 The majority of rivers were electrofished once each year, but some were sampled more
15
16 161 than once or had multiple sample sites. In these cases, a mean annual density was
17
18 162 calculated for each reach (see Appendix 1 for the frequency of sampling within each
19
20 163 river). Densities were log transformed to achieve normality and homogenise variances.
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26 165 Electrofishing sites were matched to water chemistry samples based on their proximity,
27
28 166 geology and stream order. Electrofishing reaches without comparable water chemistry
29
30 167 data (n = 14) were excluded from any analysis of fisheries trends against chemical and
31
32 168 climatic variables.
33

34 169

35
36 170 *Water chemistry*

37
38 171 Data on chemical quality, analysed by standard methods, were obtained from the
39
40 172 Environment Agency Water Management Information System (WMIS) database (SCA,
41
42 173 1978, 1979, 1981, 1988). Ammoniacal nitrogen (mg/l), dissolved oxygen (mg/l),
43
44 174 Biological Oxygen Demand (BOD [ATU]) (mg/l) and pH were monitored monthly
45
46 175 throughout all years of the study except for 1993. The total concentration of ammonium
47
48 176 salts (NH₄⁺) and free ammonia (NH₃) was determined from the reaction of ammonia
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4 177 with hypochlorite to form monochloramine and measured colorimetrically at 656nm as a
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6 178 blue indo-phenol complex using a Discrete Analyser - Aqua 800/Konelab 30
7
8 179 (SCA, 1981). Dissolved oxygen concentration was measured by the Winkler manual
9
10 180 titration method (SCA, 1979). The Biochemical Oxygen Demand (BOD) measured the
11
12 181 uptake of dissolved oxygen by a sample during 5 days at 20°C in the dark and was
13
14 182 analysed via a SKALAR automated system in the presence of allylthiourea (ATU) to
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16 183 suppress the uptake of oxygen by ammonia (SCA, 1988). pH was measured
17
18 184 electrometrically with a glass electrode WTW530 pH meter (SCA, 1978).
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24 185
25 186 Chemical samples were defined as either 'summer' (April - September) and 'winter'
26
27 187 (October - March), and mean calculated for the seasons antecedent to electrofishing.
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29 188 Missing values were replaced, where possible, with the mean for the appropriate year,
30
31 189 season and river reach.
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36 191 *Climatic variables*

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38 192 Climatic data came from several sources. To assess climatic trends across the catchment
39
40 193 as a whole, mean monthly minimum (tmin), maximum (tmax) air temperatures (°C), and
41
42 194 rainfall (mm), were obtained from Ross-on-Wye (National Grid Reference (NGR) SO
43
44 195 597238; 51° 54' 40.55" N 2° 35' 8.92"), the meteorological station at which the most
45
46 196 complete daily records were available (Met Office, 2004). We supplemented these with
47
48 197 additional temperature records available from daily (1988-2004) or weekly (1982) data
49
50 198 from Llysdinam Field Centre, Newbridge-on-Wye (NGR SO 009 586; 53° 12' 59" N
51
52 199 3°27' 3" W), directly adjacent to the river temperature sites (see below). Fewer data were
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3 200 available from stream or river temperatures, but extensive studies indicate that these can
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5 201 be modelled as a reasonable approximation using air temperature: while local factors
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7 202 such as groundwater inputs, evaporative cooling, shading and discharge affect the exact
8
9 203 nature of their inter-relationship, mean air and stream temperatures are closely correlated
10
11 204 over weekly to monthly time steps because both air and water are warmed by similar
12
13 205 processes (Webb, Clack and Walling 2003; Caissie 2006; Durance and Ormerod 2009).
14
15 206 As an example, between 1980 and 2003, monthly mean temperatures at Ross-on-Wye
16
17 207 explained 98% of the variation in mean monthly stream-water temperatures available
18
19 208 from the directly adjacent headwaters of the Afon Tywi with a regression slope of 0.81
20
21 209 (d.f.=294, F = 13,121, P<0.001 $r^2 = 0.97$; Durance and Ormerod 2007). This illustrated
22
23 210 that local stream temperatures tracked air temperature, but with increasing damping at
24
25 211 higher values. Calibrations between river temperature and air temperature at Llysdinam
26
27 212 available over a one-year period in 1982 at eight adjacent sites illustrated how this
28
29 213 damping effect varied between stream types, with unshaded higher-order tributaries of
30
31 214 the Wye tracking air temperature more directly than shaded low-order streams (Table 1;
32
33 215 Ormerod 1985; SO010512; SO014583; SN999569; SO033516; SN997530; SO019573;
34
35 216 SO032541; SO044487; altitudes 120-200m above sea level). We used these local
36
37 217 calibrations to estimate from the air-temperature series how stream temperature in
38
39 218 contrasting locations has varied through time. Temperatures for each salmonid sampling
40
41 219 location were further adjusted for altitude according to the environmental lapse rate of 6.5
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43 220 °C per 1000 m.
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3 222 Median winter (October -March) and summer (April - September) discharge (m^3/s) data
4
5 223 were taken from the Gwy and Hafren Flumes, operated by the Centre for Ecology and
6
7 224 Hydrology on Plynlimon, where the Wye rises ($52^\circ 27:26' \text{N}$, $3^\circ:47:46' \text{W}$). Our
8
9 225 assumption was that inter-annual trends in relative discharge here represented wider
10
11 226 regional pattern across the Wye even though the total [discharge-varied](#) between sites. We
12
13 227 validated this assumption by comparison with discharge at a gauged site on the Afon
14
15 228 Cothi, c 50km to the west in the adjacent Tywi catchment ($51^\circ 51:37' \text{N}$, $4^\circ 11:00' \text{W}$),
16
17 229 where discharge correlated highly significantly with the upper Wye ($r = 0.89$, $n = 289$
18
19 230 monthly mean values, $P < 0.0001$). Examination of other parameters to describe
20
21 231 discharge based on the flow-duration curve (e.g. 5% and 95% flow percentiles) gave
22
23 232 results that were highly inter-correlated with median discharge and equally inter-
24
25 233 correlated with variates describing inter-annual climate variability.
26
27 234
28
29 235 Because of expectations from patterns elsewhere in Wales (Durance and Ormerod 2007),
30
31 236 we investigated whether the North Atlantic Oscillation (NAO) contributed to inter-annual
32
33 237 variation in climate and temperature using [the mean difference between the normalised](#)
34
35 238 [sea level pressure over Gibraltar and the normalised sea level pressure over Southwest](#)
36
37 239 [Iceland](#). The NAO index is associated with changes in the surface westerlies across the
38
39 240 North Atlantic to Europe and represents dry, cold winters when negative and warm wet
40
41 241 winters when positive (Hurrell, 1995). [Monthly](#) NOA index values between [1984 and](#)
42
43 242 [2004](#) were obtained from the Climatic Research Unit and used to calculate summer and
44
45 243 winter means for use in the principal components analyses described below (Climatic
46
47 244 Research Unit, 2005; Osborn, 2005).

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6 246 *Data analysis*

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9 247 To establish whether salmonid populations declined through time, the effect of year on
10
11 248 their respective density was established from multi-level linear regression (also called
12
13 249 mixed effects models) using the [lme function in R 2.9 \(R Development Core Team 2009\)](#).

14
15 250 Multilevel models are increasingly adopted over repeated measures ANOVA and time-
16
17 251 series analyses in longitudinal studies (Van Der Leeden,1998; Pinheiro and Bates 2000,
18
19 252 Twisk, 2006). Models account for the dependency of observations by recognising a
20
21 253 hierarchical structure in the data whereby observations are nested within rivers in this
22
23 254 instance. This enables analysis of continuous and relatively short time series data, [such as](#)
24
25 255 [our 19 year](#) salmonid population data. We used a two-level design, whereby observations
26
27 256 were clustered within rivers in a ‘random intercept’ model that accounted for the
28
29 257 autocorrelated nature of the repeated observations within rivers (Twisk, 2006). A random
30
31 258 intercept regression model that included a random slope improved the (log likelihood) fit
32
33 259 of the model (Twisk, 2006). The correlation between the random intercept and random
34
35 260 slope was used to indicate whether rivers with high or low densities of salmonids were
36
37 261 more or less susceptible to population decline. A negative correlation would indicate that
38
39 262 rivers with a higher density of salmonids had a low slope, or less dramatic decline
40
41 263 assuming a negative relationship between density and time.

42
43
44 264 Spearman’s correlation coefficients (r_s) were calculated between water quality, climate
45
46 265 and year. We then used Principal Components Analysis (PCA) separately on the
47
48 266 correlation matrices of climatic and water quality variables, respectively for summer and
49
50 267 winter, to derive variates describing trends in environmental variation through time.
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4 268 To assess which synoptic environmental variates from PCA best explained trends in the
5
6 269 density of juvenile salmonid populations through time, we again used multi-level linear
7
8 270 regression. A two-level design, similar to that described for the assessment of the effects
9
10 271 of time on density, was adopted whereby observations were clustered within rivers in a
11
12 272 ‘random intercept’ model that accounted for the autocorrelated nature of the repeated
13
14 273 observations within rivers (Twisk, 2006). The fixed effects of each of the climatic
15
16 274 variables on salmonids density were therefore established after using random coefficients
17
18 275 for each river to model the covariance structure of the data. The inclusion of a random
19
20 276 slope into the random intercept regression model did not significantly improve fits.
21
22 277 However, there was strong evidence to support the inclusion of a first-order
23
24 278 autoregressive (AR1) term to model residual autocorrelation within rivers ($\Delta AIC = 8.0$
25
26 279 and 39.5 for salmon and trout respectively). The predicted change in density with each
27
28 280 climatic variable was estimated by examining raw variables values at the 5, 25, 75 and 95
29
30 281 percentiles of PCA scores.

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37 282 All data were transformed to reduce skew and kurtosis when appropriate. Analyses were
38
39 283 repeated for juvenile salmon (> 0+) and juvenile trout (> 0+) and Bonferroni adjustment
40
41 284 for multiple tests are reported (Quinn and Keough, 2002).

42
43
44 285

45 46 286 **Results**

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48 287

49 50 288 *Trends in salmonid density*

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52
53 289 Juvenile salmon and trout densities declined between 1985 and 2004 across the Wye
54
55 290 catchment by 50% and 67%, respectively (Figure 2, Table 2). This change was

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3 291 significant, as demonstrated by a negative regression coefficient for density of both
4
5 292 salmon and trout juvenile with year (Table 2). The correlation between the random
6
7 293 intercept and random slope was negative (salmon: -0.26, Wald Z =2.48; $p=0.013$; trout: -
8
9 294 0.28, Wald Z =2.16; $p=0.031$) indicating that rivers with higher densities of salmonids
10
11 295 had a low slope, or less dramatic decline in populations. In addition to declining trends
12
13 296 through time, populations were characterised by marked inter-annual variations (Figure
14
15 297 2).

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21
22 299 *Long-term environmental change*

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24 300 From the early 1980s, water quality generally improved across the Wye catchment, seen
25
26 301 for example in declining biochemical oxygen demand ('summer': $r_s = -0.59$ $P < 0.05$;
27
28 302 'winter' $r_s = -0.59$ $P < 0.05$) and ammonia ('summer': $r_s = -0.73$ $P < 0.01$; 'winter': $r_s = -$
29
30 303 0.39 $P < 0.05$). Average concentrations of oxygen were seldom below 95% saturation, or
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32 304 below 9-10 mg/L, and did not decrease significantly through time despite increasing
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34 305 temperature (see below). These chemical variations were well captured by single
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36 306 principal components in either winter or summer (Table 3).

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43 308 Mean air temperatures over the study area increased during the last 25 years by c 1.3 °C
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45 309 (from 8.5 to 9.8 °C), and local calibrations suggested that this would have increased river
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47 310 temperatures (Table 1; Figure 3). Thus, over the 19 years covered by data on salmonid
48
49 311 density, headwaters were estimated to have warmed in summer, annually and in winter by
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51 312 0.5, 0.6 and 0.7 °C, respectively, while larger tributaries warmed by 0.6, 0.8 and 1.0 °C.
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55 313 Estimated winter temperatures were strongly affected by the NAO in both headwaters
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3 314 (annual mean winter temperature = 5.93 ± 0.15 °C + 0.212 ± 0.065 x NAO) and larger
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5 315 tributaries (mean winter temperature = 6.40 ± 0.19 °C + 0.279 ± 0.086 x NAO), with both
6
7 316 relationships highly significant ($F_{1,24} = 10.40$, $r^2 = 0.27$, $P < 0.01$). After accounting for
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9 317 this effect, winter warming over the 19 years of the salmonid study was 1.1 and 1.4 °C in
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11 318 headwaters and larger tributaries, respectively (Figure 3).
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15 320 In contrast to temperature, discharge in the Wye has not changed directionally through
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17 321 time over the period studied, but low and high flow periods have been apparent (Figure
18
19 322 4). Nor have rainfall or insolation (as daily hours sun) changed through time (both $r_s <$
20
21 323 0.3 , $P > 0.1$). Inter-annual variations in all these climatic variables were well described in
22
23 324 PCA by single variates. Among summers, positive scores in this component reflected
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25 325 low discharge, high maximum temperatures and sunshine while negative values reflected
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27 326 increased rainfall and discharge when negative (Table 3). In winter, climatic variations
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29 327 mostly reflected warmer temperatures, higher rainfall, greater discharge and a stronger
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31 328 contribution from the NAO than in summer (Table 3).
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35 330 *Environmental correlates with salmonid density*
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41 332 Individual Spearman's correlations showed that brown trout populations declined
42
43 333 significantly with increasing maximum temperature ($r_s = -0.25$, $P=0.02$) and discharge (r_s
44
45 334 = 0.12 $P=0.02$), while salmon densities declined with increasing solar radiation ($r_s = -0.17$
46
47 335 $P=0.002$) and maximum temperature ($r_s = -0.126$ $P=0.018$). However, these individual
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49 336 relationships were weak, and multilevel regression produced stronger relationships with
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3 337 the synoptic climate variates in both species, particularly when lagged against the
4
5 338 previous summer (Table 4). Densities of both Atlantic salmon and brown trout declined
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7
8 339 with increasing scores on the index of antecedent summer climate (i.e. climate PC1),
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10 340 indicating that reductions in density were greatest following hotter, sunnier and drier
11
12 341 conditions (Table 4; Figure 5). On average, a shift across the inter-quartile range for this
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14
15 342 variate equated to a 0.3 °C increase in maximum temperature and a 10.1 mm decrease in
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18 343 monthly rainfall. This, in turn, appeared to reduce salmon densities by 1.7 salmon per
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20 344 100m² of river and 1.8 trout (per 100m² of river) respectively (Table 5), or around 17-
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22 345 20% of typical mean densities at the beginning of the study. Neither winter climate nor
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24
25 346 variates describing water quality explained significant variations in salmonid density.
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29 348 **Discussion**

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32 349 These data, collected over a 20-year period from two salmonids with contrasting life-
33
34 350 cycles, support all three of our hypotheses: both species have declined substantially and
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37 351 unequivocally across the Wye catchment, with trends and fluctuations better explained by
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39 352 climatic factors than any other variable examined. Of considerable importance, changes
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41 353 in both migratory Atlantic salmon and non-migratory brown trout populations appeared
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43
44 354 to be linked to synoptic climatic effects, with both species' populations declining when
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46 355 increasing summer temperature was combined with reduced discharge. While factors at
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48
49 356 other scales might affect salmon population and demographics, such as at-sea survival or
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51 357 exploitation through commercial fishing (e.g. Gee and Milner, 1980; Finney *et al.*, 2000;
52
53 358 McFarlane *et al.*, 2000; Quinn *et al.*, 2006; Ruggerone *et al.*, 2007), within-catchment
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56 359 processes affecting recruitment or survival must also be important (Rieman *et al.*, 2001;
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4 360 Regetz, 2003). Local water-quality effects in the Wye system include pollutants such as
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6 361 pyrethroids (Moore and Waring, 2001), episodic acidification in the upper catchment
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8 362 (Lewis et al. 2007) and eutrophication in the lower catchment (Clews and Ormerod
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10 363 2009), but these effects have all abated through time and so cannot explain population
11
12 364 reduction (Ormerod and Durance 2009). Notwithstanding the important caveat that our
13
14 365 analysis is based on correlation, climatic effects are the most plausible explanation for the
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16 366 trends and fluctuations observed, as well as the best statistical explanation. A reduction
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18 367 in commercial net fisheries in UK and Ireland over the study period also supports this
19
20 368 assertion. We note here that, although effects on both brown trout and salmon in our
21
22 369 analysis were apparently captured by the same broad climatic variables, the exact
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24 370 processes involved could differ between these two species, not least because of their
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26 371 different habitat requirements within stream systems (Armstrong et al., 2003).
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34 373 One important factor to consider in assessing long-term population data under varying
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36 374 climatic conditions is that temperature can affect the efficiency of electrofishing gear.
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38 375 Such effects could, in turn, potentially confound any putative effects of increasing
39
40 376 temperature on population estimates. However, the effects of a 1°C temperature increase
41
42 377 on capture efficiency are likely to be far smaller than the declines observed both salmon
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44 378 (50%) and trout juveniles (67%) in this study: the conductivity of stream water is reduced
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46 379 by only 2% per °C (Bohlin *et al.* 1989). Alabaster and Hartley (1962) described the
47
48 380 impact of conductivity on the percentage of a fish population caught by direct current
49
50 381 electrofishing according to the regression equation $y = 0.27x - 9.6$, where y is the
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52 382 percentage catch, and x is the conductivity ($\mu\text{S cm}^{-1}$) of the water. In 2003, the *in situ*
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3 383 conductivity was measured across streams within the Wye catchment and ranged from
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5 384 161 to 352 $\mu\text{S cm}^{-1}$. According to Alabaster and Hartley's (1962) equation, an increase in
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8 385 temperature of 1°C would increase the percentage of the fish population caught, rather
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10 386 than decreasing it, but by just 0.9 to 1.9 % over the range of conductivities encountered in
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12 387 the Wye. In addition to altering the stream conductivity, temperature can also affect fish
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14
15 388 behaviour and physiology (Bohlin *et al.* 1989). At higher water temperatures, fish are
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17 389 more likely to avoid sampling gear due to an increased metabolism and associated
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20 390 capacity for movement (Hayes and Baird 1994). Conversely, behaviours such as fish
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22 391 burrowing into the substrate at low temperatures may also prevent capture, and floatation
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24 392 rates are greater in warmer water thus possibly offsetting the effects of the former
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26
27 393 (Reynolds, 1996; Roni and Fayram 2000). These effects are currently harder to estimate
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29 394 quantitatively than temperature effects through altered conductivity.
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35 396 In locations elsewhere, there is strong evidence that climate is a key factor regulating
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37 397 salmonid populations (Beamish *et al.*, 1999; Beaugrand and Reid, 2003; Tolimieri and
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39 398 Levin, 2004; Zabel *et al.*, 2006; Walsh and Kilsby, 2007). Climatic effects on salmonids,
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41
42 399 such as those we detected, are therefore entirely consistent with expectation from current
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44 400 climatic trends, to which temperate, upland rivers appear highly sensitive (Durance and
45
46 401 Ormerod 2007; 2009). Climate-related variables, such as rainfall and temperature, can
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48 402 impact directly on the habitats preferred by salmonids, influencing their behaviour,
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50 403 growth and survival (e.g. Flebbe *et al.*, 2006; Seo *et al.*, 2006; Taylor 2008). Placed by
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52 404 classical studies of river zonation into the narrow, shallow, fast flowing, clear water,
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54 405 upstream 'trout zone' (Hawkes, 1975), the fry (0+) and juveniles (<0+) of *S. salar* and *S.*

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4 406 *trutta* require well-oxygenated ($5.0\text{--}5.5\text{ mg l}^{-1}$), cool (optimally $13\text{--}16\text{ }^{\circ}\text{C}$), relatively fast
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6 407 flowing water (approximately $10\text{--}30\text{ cm s}^{-1}$ and $20\text{--}50\text{ cm s}^{-1}$ respectively), and
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8 408 inhabiting deeper water as they grow (Armstrong *et al.*, 2003). Conditions in the Wye,
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10 409 particularly in larger unshaded tributaries, have increasingly exceeded this temperature
11
12 410 optimum over the last 20 years (see Figure 3). As poikilotherms, the foraging behaviour
13
14 411 and habitat use of salmonids is strongly influenced by temperature (Armstrong *et al.*,
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16 412 2003). Elevated temperatures in temperate climates may extend the growing season for
17
18 413 salmonids while also increasing metabolic demands and food requirements while
19
20 414 possibly also increasing susceptibility to disease (Elliot *et al.*, 1998). For example, in
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22 415 alpine streams in Switzerland increased water temperatures induced higher incidences of
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24 416 proliferative kidney disease in brown trout at higher altitudes (Hari *et al.*, 2006).

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33 418 Changes in the intensity and frequency of rainfall affect river-flow regimes and have
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35 419 implications for the accessibility, permanence and suitability of habitats, and hence
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37 420 salmonid distribution (Armstrong *et al.*, 2003; Hakala and Hartman, 2004). Recent
38
39 421 experimental manipulations of flow to mimic low summer discharge in a British chalk
40
41 422 stream produced results consistent with our data from the Wye, showing how increased
42
43 423 mortality of both salmon and trout under low summer flow reflected reduction in habitat
44
45 424 availability (Riley, *et al.*, 2009). Interesting in our study was that low-flow and warming
46
47 425 effects both appeared to contribute to population reduction, and again this is consistent
48
49 426 with previous observation. For example, in the Upper Rhône River, low flow and high
50
51 427 temperature favoured thermophilic fish species (e.g. *Leuciscus cephalus* and *Barbus*
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53 428 *barbus*) at the expense of northern, cold-water fish species (e.g. *Leuciscus leuciscus*)

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2
3 429 (Daufresne *et al.*, 2004). One possibility that requires further investigation is that the
4
5 430 availability of thermal refuges in rivers declines at low flow in ways that prevent
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8 431 salmonids from finding and occupying locally cooler micro-environments (Clark, Webb
9
10 432 and Ladle 1999; Arscott, Tockner and Ward 2001; Breau *et al.* 2007). The risk of such
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12 433 effects is supported by evidence that i).small-scale thermal gradients increase in rivers
13
14 434 with increasing depth (as well as with lateral shade; Clark *et al.* (1999) and ii) increased
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16 435 discharge and depth increase thermal mass and thermal inertia such that rivers track air
17
18 436 temperature less closely as flow increases (Webb *et al.* 2003). Further work is now
19
20 437 required to establish exactly where in river systems, when and how combined low flows
21
22 438 and elevated temperatures might be most damaging to salmonids.
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30 440 One technical component of our analytical approach is that it appears to assume linear
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32 441 responses between salmon, trout and environmental processes affecting populations.
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34 442 However, species do not necessarily respond linearly to environmental gradients
35
36 443 (Armstrong *et al.*, 2003).. For example, growth rates are temperature-dependent and
37
38 444 reach an asymptotic optima at 15.9 and 13.1 °C in salmon and trout respectively (Elliott
39
40 445 and Hurley, 1995, 1997). To assess the possibility of non-linear relationships between
41
42 446 climate and salmon or trout densities, we re-fitted models using generalised additive
43
44 447 mixed modelling using the GAMM approach of Wood (2006) *Generalized Additive*
45
46 448 *Models*, Chapman & Hall) – i.e. employing generalised cross validation to select an
47
48 449 appropriate degree of smoothing for each variable. There was insufficient evidence that
49
50 450 the relationships between salmon, trout and summer climate or any measure of water
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52 451 quality were non-linear, selecting a linear fit for the model. The linear models presented
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4 452 here therefore provide the best current guide to the potential responses of salmonids to
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6 453 climatic variation within their optimal range. Interestingly, there was some evidence of a
7
8 454 weak non-linear relationship between trout, salmon and winter climate, but it arose only
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10 455 with lags of > 1-2 winters before the time of sampling, and moreover was not statistically
11
12 456 significant after modelling residual autocorrelation. We therefore suggest that such winter
13
14 457 climatic effects in the Wye, either alone or in combination with summer effects, would
15
16 458 warrant further investigation only when a longer data run is available. Salmonid life
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18 459 cycles operate over multiple years and are complex, involving migration to accommodate
19
20 460 the different habitat preferences of each life-stage (see Crisp, 1996; Armstrong *et al.*,
21
22 461 2003). For example, the life cycle of salmon in the Wye system require at least 2 years
23
24 462 from egg to adult spawner, and more in the case of multi-sea-winter fish (>3 years) which
25
26 463 made up approximately 90% of rod catches in 1977 (Edwards and Brooker, 1982).
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28 464 Climatic effects operating on salmonids are therefore integrated across the entire lifespan
29
30 465 of the fish as well as that of the previous generation. The numbers of Atlantic Salmon
31
32 466 spawners returning to the Wye have declined over the study period – notably for the
33
34 467 number and proportion of multi-sea-winter fish (Environment Agency, 2003a). At least in
35
36 468 this species (as opposed to the Wye's brown trout), the influence of climatic and
37
38 469 anthropogenic factors affecting potential spawners in the marine environment cannot be
39
40 470 discounted as an influence on the decline of salmon juveniles (Kennedy and Crozier
41
42 471 1993; Potter *et al.*, 2003; Jonsson and Jonsson, 2004). Notwithstanding these
43
44 472 possibilities, the period between emergence and the establishment of feeding territories in
45
46 473 salmonids is critical, and this is the period we were particularly interested in capturing
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48 474 when testing hypotheses about summer climate (Armstrong *et al.*, 2003; Nislow *et al.*,
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3 475 2004). Climatic variables presented here operated over this critical period in the
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5 476 development of the juvenile salmonids in the Wye. Correlations between climatic
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7 477 variables and salmon densities were generally greater for the preceding year when
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9 478 considered against the each of the preceding 7 years respectively. *The relatively short*
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11 479 *time-lags over which climate variables were found to affect salmon density significantly*
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13 480 *imply that freshwater condition rather than marine factors affected the variations*
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15 481 *observed in juveniles.*
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21 483 *Future climatic effects and their management*

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26 484 If the effects detected in the Wye are substantiated by surveys or experiments elsewhere,
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28 485 there are clearly potential implications for the future status of salmonids under climate
29
30 486 change. This has particular importance in the case of Atlantic salmon given its position
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32 487 on the EU Habitats Directive (92/43/EEC) and its relevance to the designation of rivers as
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34 488 'Special Areas of Conservation as part of the 'Natura 2000' network. The UK climate is
35
36 489 likely to warm between 2-5 °C by 2080 (Hulme *et al.*, 2002), with winters in western
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38 490 Britain wetter but summers drier (Conway, 1998; Hulme *et al.*, 2002). Effects of this
39
40 491 magnitude are already developing in British rivers (Durance and Ormerod 2007; 2009),
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42 492 while studies in the Upper Wye suggest that the occurrence and amount of precipitation
43
44 493 will decrease in summer and autumn, while evapotranspiration will increase, resulting in
45
46 494 more frequent 'low flows' (Pilling and Jones, 2002). Extreme drought events, as
47
48 495 experienced in 1990, 1995, 2003 and also in 1976 with catastrophic effects on salmonids
49
50 496 (Edwards and Brooker, 1982), are likely to occur at increased frequency. Given the trends
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52 497 recorded here, changes of this type would be detrimental to salmonid populations unless
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4 498 adaptive management actions are taken to offset the worst effects. Maintaining river
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6 499 discharge through reducing abstraction and increasing compensation flow will be
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8 500 important, while the use of riparian shade to reduce the effects of adverse summer
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10 501 temperatures is also gaining favour (Rutherford *et al.*, 2004; Watanabe *et al.*, 2005;
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12 502 Ormerod 2009). Our own evidence supports this effect (Figure 3), while similar results
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14
15 503 elsewhere suggests that riparian shade can reduce summer temperature at least as
16
17 504 effectively as the effect of groundwater damping on chalk-fed rivers (Table 6). On this
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19
20 505 basis, riparian shading could become a critical tool in maintaining salmonids in the
21
22 506 southern part of their current European range.

23
24
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29
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3 **796** **Table 1:** Generalised regression relationships ($y = a + bx$) between weekly mean stream
4 **797** temperature at sites in the catchment of the Welsh River Wye and air temperature at
5 **798** Newbridge-on Wye (After Ormerod 1985). Regressions are shown respectively for
6 **799** lower-order headwaters with riparian shading and larger-order main channels with less
7 **800** riparian vegetation.
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	$a \pm 95\% \text{ CI}$	$b \pm 95\% \text{ CI}$	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

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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 \pm SE), 95% confidence intervals (CI) and corresponding ρ -values.

a) Salmon				
Variable	Estimate (SE)	t	ρ	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	ρ	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

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810 **Table 3.** Principal Component (PC) axes representing variation in ‘climatic variables’
 811 and ‘water quality’ relevant to the Wye system recorded between 1985 and 2000 in
 812 summer (April - September) and winter (October - March), respectively. Eigenvectors
 813 indicate the loading of variables on the first PC axis extracted in Principal Component
 814 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

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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
Welsh rivers and streams	
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

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3 842 Figure Legends

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5 844 **Figure 1.** Location of electrofishing sites within the catchment of the Welsh River Wye
6 845 (small symbols), showing also those with chemical data (larger symbols).

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8 847 **Figure 2.** Standardised (mean z scores \pm SE) relative densities of juvenile (>0+) salmon
9 848 and trout juveniles averaged across tributaries of the Welsh River Wye, 1985 – 2004. N
10 849 indicates the number of rivers contributing to mean annual density in each year.

11 850

12 851 **Figure 3.** Long-term trends the annual (a: $y = 0.0413x - 70.759$ ●; $y = 0.0314x - 52.637$
13 852 ○; $r^2 = 0.38$), summer (b; $y = 0.0339x - 50.414$ ●; $y = 0.0257x - 37.194$ ○; $r^2 = 0.1164$)
14 853 and winter (c; $y = 0.0504x - 93.782$ ●; $y = 0.0383x - 70.113$ ○; $r^2 = 0.1411$) temperature
15 854 of tributaries of the River Wye as estimated from trends in air temperature using
16 855 generalised calibrations respectively from three larger, unshaded tributaries (●) and five
17 856 shaded headwaters (○). Panel d) shows trends in residual winter temperature after
18 857 accounting for the significant of the NAO (see text) ($y = 0.0732x - 145.95$ ●; $y = 0.0556x$
19 858 - 110.78 ○; $r^2 = 0.4264$).

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21 860 **Figure 4.** Long-term variations in discharge during summer (a) and winter (b) at the CEH
22 861 Hafren Flume, Plynlimon.

23 862

24 863 **Figure 5.** Densities of >0+ salmon (a) and brown trout (b) per 100m² reach averaged
25 864 (mean \pm SE) across tributaries of the Wye catchment in each year plotted against an index
26 865 on antecedent summer climate. This is derived as the first component from a Principal
27 866 Components Analysis (PC) on climatic variables during the (see Table 3).

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3 870 **Appendix 1.** Frequency of sampling of salmonids in the Wye catchment 1985-2004.
4 871 Years which included quantitative sampling of rivers are indicated by *. Monitoring was
5 872 not undertaken in 1996. Rivers which were split into upstream and downstream reaches
6 873 according to proximity, geology and stream order are indicated by upstream 'u/s' and
7 874 downstream 'd/s', respectively.
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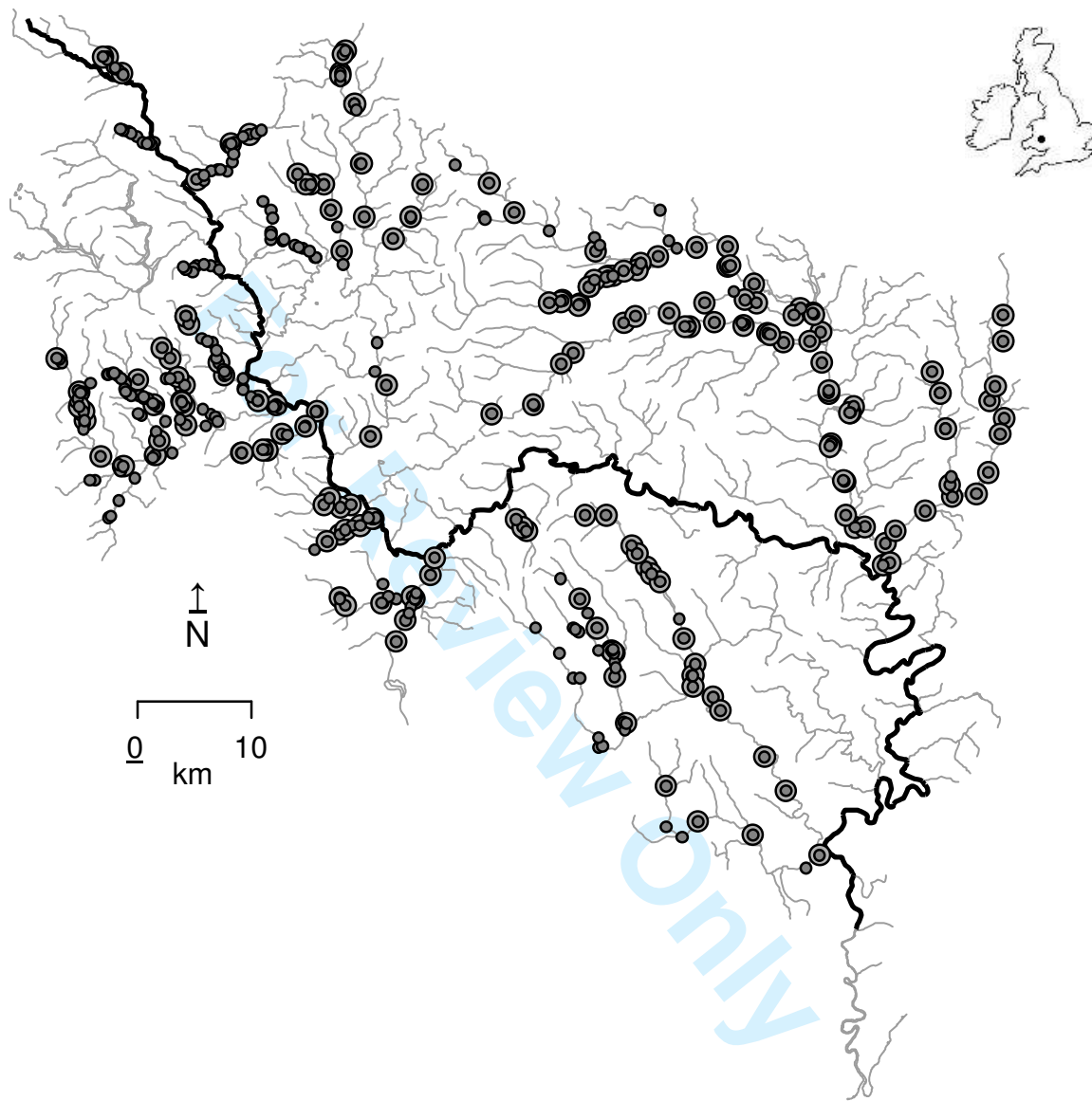
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River	Year																	
	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1997	1998	1999	2000	2002	2003	2004
Aran	2*	2	1	1	1	1	1	1	1	1	1	3	0	3	0	1*	3*	1*
Arrow (d/s)	2	2	1*	1	0	0	0	0	0	0	0	1	4*	1	0	1*	2*	1*
Arrow (u/s)	4	4	3*	3	4*	4*	4*	3*	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*
Triffwyd	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

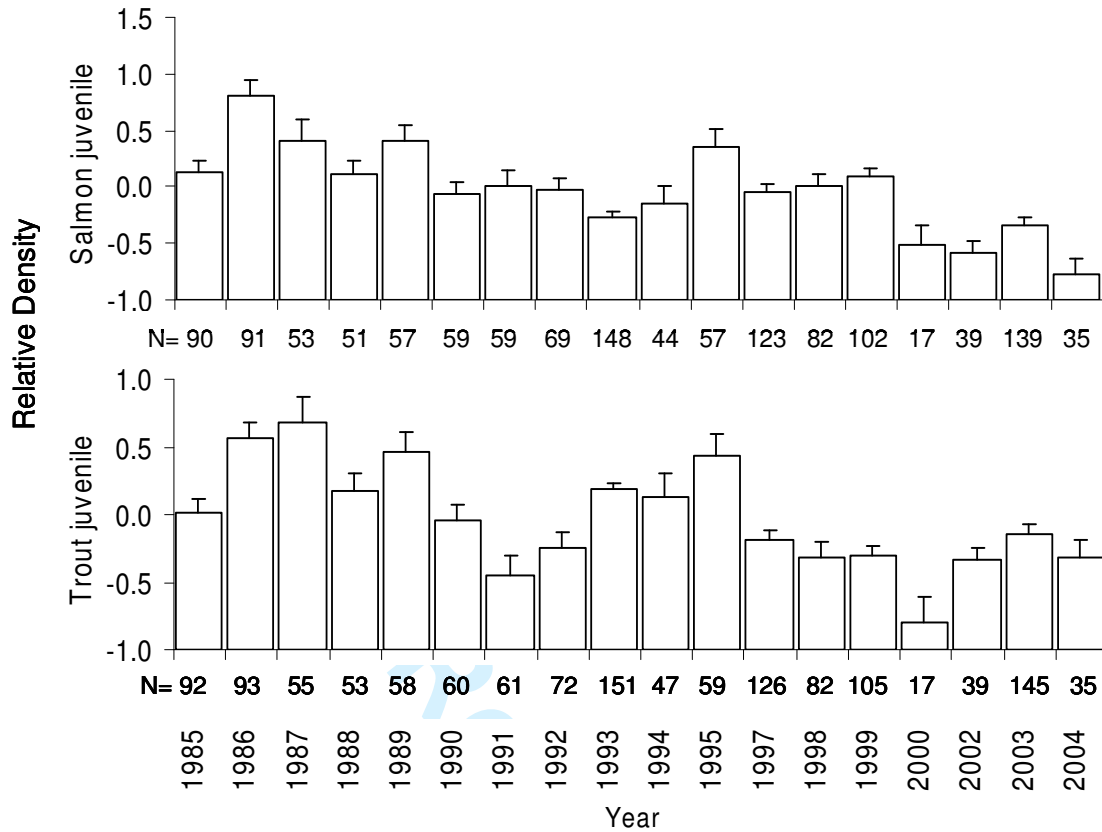
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Figure 1



Global Change Biology GCB-09-0020 revised



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882 Figure 2

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Global Change Biology GCB-09-0020 revised

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Figure 3:

For Review Only

Global Change Biology GCB-09-0020 revised

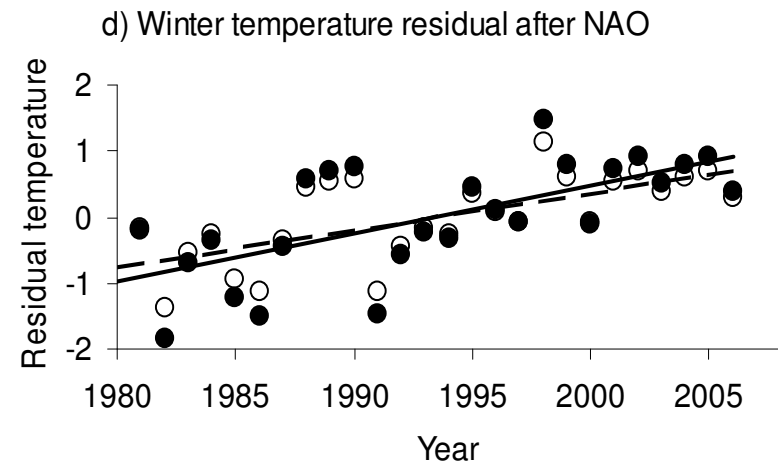
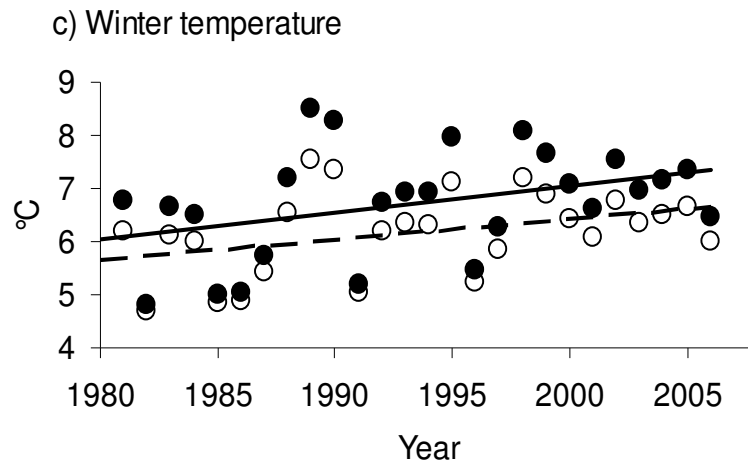
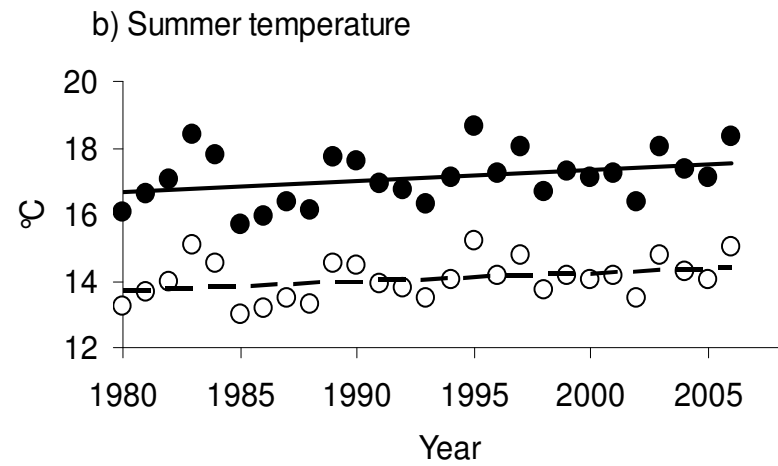
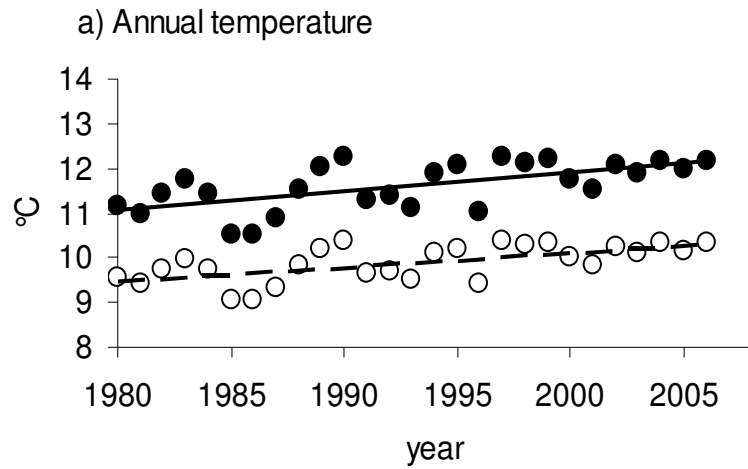


Figure 4

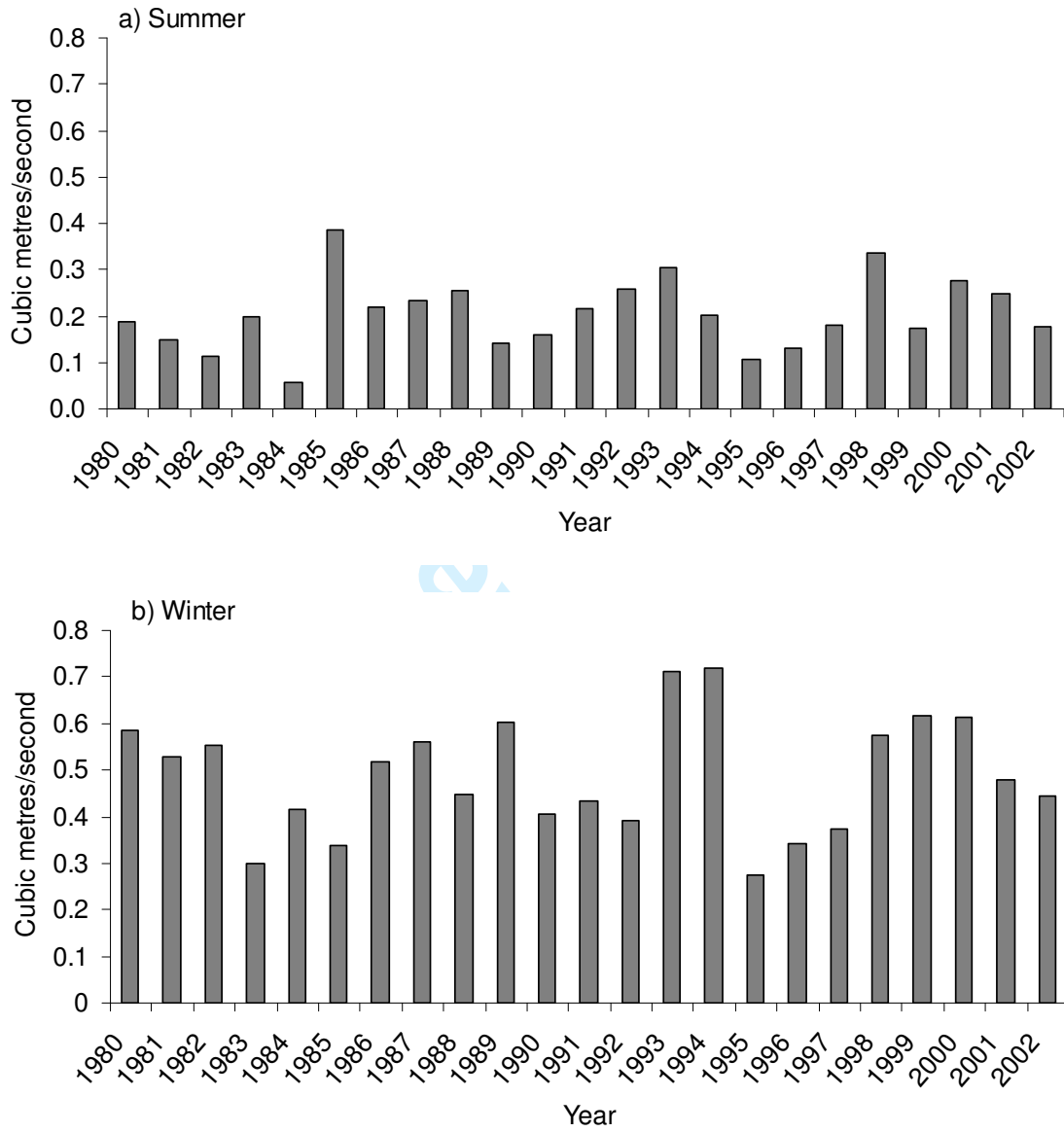


Figure 5

