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

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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.

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

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

Key population factors almost certainly act in combination (Marschall and Crowder, 1996; Parrish et al., 1998; Milner et al., 2003), with density-dependence, environmental or demographic stochasticity, and land or river management all implicated in current declining trends in salmonid populations (Wilzbach et al., 1998; Parrish et al., 1998; Ormerod, 2003; Zabel et al., 2006). Effects might also be scale-dependent. At river reach scales, habitat quality influences the abundance of salmonids by direct provision of refugia and food resources, so that riparian or in-stream degradation can affect local carrying capacity (Borsuk, et al., 2006). More widely, across river catchments, barriers to migration, habitat fragmentation, diffuse pollutants, agricultural intensification and industrialization have all had negative effects (Parrish et al., 1998; Ormerod, 2003; Suttle et al., 2004; Dudgeon et al., 2006). Finally, over regional scales, direct exploitation and disease can alter salmonid populations (Bowker et al., 1998; Hari et al., 2006; Quinn et
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 (Aprahamian 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
– for example through drought – can also have large effects on salmonids (Elliott et al. 1997)

Although long-term data sets are increasingly available through which explanations for variations among salmonids might be assessed, long-term evaluations of climatic effects through time or between years are still few (Thomas, 1996; Bjornstad and Grenfell, 2001; Daufresne et al., 2004; Hulme, 2005; Crozier and Zabel, 2006). This is particularly the case where species with and without marine phases in their life cycle, such as Atlantic salmon and brown trout, have been compared in the same catchment. The River Wye, in Wales, western Britain, provides a particularly important case study that allows an evaluation of trends in both these species. Here, brown trout are non-anadromous, unlike some other UK rivers where this species has sea-run components, thus enabling a contrast with migratory salmon (Edwards and Brooker, 1982). The Wye was traditionally one of the best salmon angling rivers in the UK, so that long-term and wide scale data on juvenile populations are available (Gee, Milner and Hemworth 1978a,b). However, in recent decades, there have been marked declines in stocks of Atlantic salmon and brown trout (Gee and Milner, 1980; Gough et al., 1992; Environment Agency, 2003 a and b).

Because riparian and in-stream management to benefit salmonids has been attempted, and some aspects of water quality have improved, there are few local, catchment-scale factors that might explain this decline (Clews and Ormerod 2009; Clews, Vaughan & Ormerod 2010).
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.
Partly because of its importance for Atlantic salmon the Wye river system is both a Site of Special Scientific Interest (SSSI) and Special Area of Conservation (SAC) under the EU Habitats Directive (Directive 92/43/EEC) (Joint Nature Conservancy Committee, 2004).

**Materials and Methods**

**Overall study design**

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

**Salmonid data**

Juvenile salmonid data were derived by electrofishing by the Environment Agency, Wales (Environment Agency and CEFAS, 2004) during summer (April to October) most frequently in August (61% of samples). Since post young-of-the-year (> 0+) survival, unlike young-of-the-year (0+) survival, is relatively constant over the months of May to September we combined all available data into an annual mean for each stream reach (Juanes et al. 2000). Quantitative electrofishing surveys (29% of samples) involved three electrofishing runs per reach (approx. 50m) of river to yield a population estimate as density of fish per m$^2$ of river based on catch-depletion. Semi-quantitative surveys (71% of samples) involved just one run per site. Equations used to estimate equivalent 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% 5.4 standard 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 form the reaction of ammonia
with hypochlorite to form monochloramine and measured colorimetrically at 656nm as a blue indo-phenol complex using a Discrete Analyser - Aqua 800/Konelab 30 (SCA, 1981). Dissolved oxygen concentration was measured by the Winkler manual titration method (SCA, 1979). The Biochemical Oxygen Demand (BOD) measured the uptake of dissolved oxygen by a sample during 5 days at 20°C in the dark and was analysed via a SKALAR automated system in the presence of allylthiourea (ATU) to suppress the uptake of oxygen by ammonia (SCA, 1988). pH was measured electrometrically with a glass electrode WTW530 pH meter (SCA, 1978).

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

Climatic variables

Climatic data came from several sources. To assess climatic trends across the catchment as a whole, mean monthly minimum (tmin), maximum (tmax) air temperatures (°C), and rainfall (mm), were obtained from Ross-on-Wye (National Grid Reference (NGR) SO 597238; 51° 54' 40.55" N 2° 35' 8.92"), the meteorological station at which the most complete daily records were available (Met Office, 2004). We supplemented these with additional temperature records available from daily (1988-2004) or weekly (1982) data from Llysdinam Field Centre, Newbridge-on-Wye (NGR SO 009 586; 53° 12' 59" N 3°27' 3" W), directly adjacent to the river temperature sites (see below). Fewer data were
available from stream or river temperatures, but extensive studies indicate that these can be modelled as a reasonable approximation using air temperature: while local factors such as groundwater inputs, evaporative cooling, shading and discharge affect the exact nature of their inter-relationship, mean air and stream temperatures are closely correlated over weekly to monthly time steps because both air and water are warmed by similar processes (Webb, Clack and Walling 2003; Caissie 2006; Durance and Ormerod 2009). As an example, between 1980 and 2003, monthly mean temperatures at Ross-on-Wye explained 98% of the variation in mean monthly stream-water temperatures available from the directly adjacent headwaters of the Afon Tywi with a regression slope of 0.81 (d.f.=294, F = 13,121, P<0.001 r² = 0.97; Durance and Ormerod 2007). This illustrated that local stream temperatures tracked air temperature, but with increasing damping at higher values. Calibrations between river temperature and air temperature at Llysdinam available over a one-year period in 1982 at eight adjacent sites illustrated how this damping effect varied between stream types, with unshaded higher-order tributaries of the Wye tracking air temperature more directly than shaded low-order streams (Table 1; Ormerod 1985; SO010512; SO014583; SN999569; SO033516; SN997530; SO019573; SO032541; SO044487; altitudes 120-200m above sea level). We used these local calibrations to estimate from the air-temperature series how stream temperature in contrasting locations has varied through time. Temperatures for each salmonid sampling location were further adjusted for altitude according to the environmental lapse rate of 6.5 °C per 1000 m.
Median winter (October - March) and summer (April - September) discharge (m$^3$/s) data were taken from the Gwy and Hafren Flumes, operated by the Centre for Ecology and Hydrology on Plynlimon, where the Wye rises (52° 27:26’N, 3°:47:46’ W). Our assumption was that inter-annual trends in relative discharge here represented wider regional pattern across the Wye even though the total discharge varied between sites. We validated this assumption by comparison with discharge at a gauged site on the Afon Cothi, c 50km to the west in the adjacent Tywi catchment (51° 51:37’ N, 4° 11:00’ W), where discharge correlated highly significantly with the upper Wye ($r = 0.89$, $n = 289$ monthly mean values, $P < 0.0001$). Examination of other parameters to describe discharge based on the flow-duration curve (e.g. 5% and 95% flow percentiles) gave results that were highly inter-correlated with median discharge and equally inter-correlated with variates describing inter-annual climate variability.

Because of expectations from patterns elsewhere in Wales (Durante and Ormerod 2007), we investigated whether the North Atlantic Oscillation (NAO) contributed to inter-annual variation in climate and temperature using the mean difference between the normalised sea level pressure over Gibraltar and the normalised sea level pressure over Southwest Iceland. The NAO index is associated with changes in the surface westerlies across the North Atlantic to Europe and represents dry, cold winters when negative and warm wet winters when positive (Hurrell, 1995). Monthly NAO index values between 1984 and 2004 were obtained from the Climatic Research Unit and used to calculate summer and winter means for use in the principal components analyses described below (Climatic Research Unit, 2005; Osborn, 2005).
Data analysis

To establish whether salmonid populations declined through time, the effect of year on their respective density was established from multi-level linear regression (also called mixed effects models) using the `lme` function in R 2.9 (R Development Core Team 2009). Multilevel models are increasingly adopted over repeated measures ANOVA and time-series analyses in longitudinal studies (Van Der Leeden, 1998; Pinheiro and Bates 2000, Twisk, 2006). Models account for the dependency of observations by recognising a hierarchical structure in the data whereby observations are nested within rivers in this instance. This enables analysis of continuous and relatively short time series data, such as our 19 year salmonid population data. We used a two-level design, 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). A random intercept regression model that included a random slope improved the (log likelihood) fit of the model (Twisk, 2006). The correlation between the random intercept and random slope was used to indicate whether rivers with high or low densities of salmonids were more or less susceptible to population decline. A negative correlation would indicate that rivers with a higher density of salmonids had a low slope, or less dramatic decline assuming a negative relationship between density and time.

Spearman’s correlation coefficients ($r_s$) were calculated between water quality, climate and year. We then used Principal Components Analysis (PCA) separately on the correlation matrices of climatic and water quality variables, respectively for summer and 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; \( \rho =0.013 \); trout: -0.28, Wald Z =2.16; \( \rho =0.031 \)) 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...
(annual mean winter temperature = 5.93 ± 0.15 °C + 0.212 ± 0.065 x NAO) and larger tributaries (mean winter temperature = 6.40 ± 0.19 °C + 0.279 ± 0.086 x NAO), with both relationships highly significant ($F_{1,24} = 10.40$, $r^2 = 0.27$, $P < 0.01$). After accounting for this effect, winter warming over the 19 years of the salmonid study was 1.1 and 1.4 °C in headwaters and larger tributaries, respectively (Figure 3).

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

Environmental correlates with salmonid density

Individual Spearman’s correlations showed that brown trout populations declined significantly with increasing maximum temperature ($r_s = -0.25$, $P=0.02$) and discharge ($r_s = 0.12$, $P=0.02$), while salmon densities declined with increasing solar radiation ($r_s = -0.17$, $P=0.002$) and maximum temperature ($r_s = -0.126$, $P=0.018$). However, these individual 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 100m$^2$ of river and 1.8 trout (per 100m$^2$ 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;...
Regetz, 2003). Local water-quality effects in the Wye system include pollutants such as pyrethroids (Moore and Waring, 2001), episodic acidification in the upper catchment (Lewis et al. 2007) and eutrophication in the lower catchment (Clews and Ormerod 2009), but these effects have all abated through time and so cannot explain population reduction (Ormerod and Durance 2009). Notwithstanding the important caveat that our analysis is based on correlation, climatic effects are the most plausible explanation for the trends and fluctuations observed, as well as the best statistical explanation. A reduction in commercial net fisheries in UK and Ireland over the study period also supports this assertion. We note here that, although effects on both brown trout and salmon in our analysis were apparently captured by the same broad climatic variables, the exact processes involved could differ between these two species, not least because of their different habitat requirements within stream systems (Armstrong et al., 2003).

One important factor to consider in assessing long-term population data under varying climatic conditions is that temperature can affect the efficiency of electrofishing gear. Such effects could, in turn, potentially confound any putative effects of increasing temperature on population estimates. However, the effects of a 1°C temperature increase on capture efficiency are likely to be far smaller than the declines observed both salmon (50%) and trout juveniles (67%) in this study: the conductivity of stream water is reduced by only 2% per °C (Bohlin et al. 1989). Alabaster and Hartley (1962) described the impact of conductivity on the percentage of a fish population caught by direct current electrofishing according to the regression equation \( y = 0.27x - 9.6 \), where \( y \) is the percentage catch, and \( x \) is the conductivity (\( \mu S \ cm^{-1} \)) of the water. In 2003, the *in situ*
conductivity was measured across streams within the Wye catchment and ranged from 161 to 352 µS 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.
trutta require well-oxygenated (5.0–5.5 mg l$^{-1}$), cool (optimally 13-16 °C), relatively fast flowing water (approximately 10–30 cm s$^{-1}$ and 20–50 cm s$^{-1}$ respectively), and inhabiting deeper water as they grow (Armstrong et al., 2003). Conditions in the Wye, particularly in larger unshaded tributaries, have increasingly exceeded this temperature optimum over the last 20 years (see Figure 3). As poikilotherms, the foraging behaviour and habitat use of salmonids is strongly influenced by temperature (Armstrong et al., 2003). Elevated temperatures in temperate climates may extend the growing season for salmonids while also increasing metabolic demands and food requirements while possibly also increasing susceptibility to disease (Elliot et al., 1998). For example, in alpine streams in Switzerland increased water temperatures induced higher incidences of proliferative kidney disease in brown trout at higher altitudes (Hari et al., 2006).

Changes in the intensity and frequency of rainfall affect river-flow regimes and have implications for the accessibility, permanence and suitability of habitats, and hence salmonid distribution (Armstrong et al., 2003; Hakala and Hartman, 2004). Recent experimental manipulations of flow to mimic low summer discharge in a British chalk stream produced results consistent with our data from the Wye, showing how increased mortality of both salmon and trout under low summer flow reflected reduction in habitat availability (Riley, et al., 2009). Interesting in our study was that low-flow and warming effects both appeared to contribute to population reduction, and again this is consistent with previous observation. For example, in the Upper Rhône River, low flow and high temperature favoured thermophilic fish species (e.g. Leuciscus cephalus and Barbus barbus) at the expense of northern, cold-water fish species (e.g. Leuciscus leuciscus)
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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.,
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
adaptive management actions are taken to offset the worst effects. Maintaining river
discharge through reducing abstraction and increasing compensation flow will be
important, while the use of riparian shade to reduce the effects of adverse summer
temperatures is also gaining favour (Rutherford et al., 2004; Watanabe et al., 2005;
Ormerod 2009). Our own evidence supports this effect (Figure 3), while similar results
elsewhere suggests that riparian shade can reduce summer temperature at least as
effectively as the effect of groundwater damping on chalk-fed rivers (Table 6). On this
basis, riparian shading could become a critical tool in maintaining salmonids in the
southern part of their current European range.

Acknowledgements

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Graham Lightfott, Prof Bruce Webb and two anonymous reviewers provided helpful
comments on the manuscript. EC was funded by the Wye and Usk Foundation, and we
thank Dr Stephen Marsh-Smith. IPV was supported by Fellowship of the UK Research
Councils and ID was funded by the Natural Environment Research Council through a
Daphne Jackson Fellowship.
References


Arscott DB, Tockner K, Ward JV (2001) Thermal heterogeneity along a braided floodplain river (Tagliamento River, northeastern Italy). *Canadian Journal of Fisheries and Aquatic Sciences, 58*, 2359-2373


Hulme, M, Jenkins, GJ, Lu, X, Turnpenny, JR, Mitchell, TD, Jones, RG, Lowe, J, Murphy, JM, Hassell, D, Boorman, P, McDonald, R and Hill, S (2002) Climate change scenarios for the United Kingdom: the UKCIP02 Scientific report. April 2002., Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia, Norwich, UK.
Global Change Biology GCB-09-0020 revised


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.

<table>
<thead>
<tr>
<th></th>
<th>$a \pm 95% \text{ CI}$</th>
<th>$b \pm 95% \text{ CI}$</th>
<th>$N$</th>
<th>100.$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Headwaters</td>
<td>3.40 ± 0.40</td>
<td>0.715 ± 0.039</td>
<td>159</td>
<td>89.1</td>
</tr>
<tr>
<td>Main channels</td>
<td>3.07 ± 0.77</td>
<td>0.942 ± 0.075</td>
<td>77</td>
<td>89.3</td>
</tr>
</tbody>
</table>
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 ρ-values.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate (SE)</th>
<th>t</th>
<th>ρ</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>34.08 (4.83)</td>
<td>7.06</td>
<td>&lt;0.001</td>
<td>24.31-43.84</td>
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<tr>
<td>Year</td>
<td>-0.02 (0.002)</td>
<td>-6.93</td>
<td>&lt;0.001</td>
<td>-0.02 - -0.01</td>
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</tbody>
</table>

b) Trout

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate (SE)</th>
<th>t</th>
<th>ρ</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>28.59 (5.4)</td>
<td>5.30</td>
<td>&lt;0.001</td>
<td>17.67-39.50</td>
</tr>
<tr>
<td>Year</td>
<td>-0.01 (0.003)</td>
<td>-5.16</td>
<td>&lt;0.001</td>
<td>-0.02 - -0.01</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Summer ‘climate’ component</th>
<th>Summer ‘water quality’ component</th>
</tr>
</thead>
<tbody>
<tr>
<td>48.9 % variance explained</td>
<td>40.3 % variance explained</td>
</tr>
<tr>
<td>Sun hours</td>
<td>0.907</td>
</tr>
<tr>
<td>Discharge m³/s</td>
<td>-0.856</td>
</tr>
<tr>
<td>Rain mm</td>
<td>-0.851</td>
</tr>
<tr>
<td>Tmin °C</td>
<td>0.081</td>
</tr>
<tr>
<td>Tmax °C</td>
<td>0.755</td>
</tr>
<tr>
<td>NAO index</td>
<td>0.278</td>
</tr>
<tr>
<td>Ammonia N mg/l</td>
<td>0.722</td>
</tr>
<tr>
<td>BOD mg/l</td>
<td>0.762</td>
</tr>
<tr>
<td>Dissolved Oxygen mg/l</td>
<td>-0.639</td>
</tr>
<tr>
<td>pH</td>
<td>0.317</td>
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</table>

<table>
<thead>
<tr>
<th>Winter ‘climate’ component</th>
<th>Winter ‘water quality’ component</th>
</tr>
</thead>
<tbody>
<tr>
<td>45.0 % variance explained</td>
<td>47.3 % variance explained</td>
</tr>
<tr>
<td>Sun hours</td>
<td>0.278</td>
</tr>
<tr>
<td>Discharge m³/s</td>
<td>0.702</td>
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<tr>
<td>Rain mm</td>
<td>0.619</td>
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<tr>
<td>Tmin °C</td>
<td>0.857</td>
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<tr>
<td>Tmax °C</td>
<td>0.885</td>
</tr>
<tr>
<td>NAO index</td>
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<tr>
<td>Ammonia N mg/l</td>
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<tr>
<td>BOD mg/l</td>
<td>0.606</td>
</tr>
<tr>
<td>Dissolved Oxygen mg/l</td>
<td>-0.696</td>
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<tr>
<td>pH</td>
<td>0.704</td>
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</tbody>
</table>
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 ± SE), 95% confidence intervals (CI) and corresponding p-values.

### a)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate (SE)</th>
<th>t</th>
<th>p</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.67 (0.04)</td>
<td>16.85</td>
<td>&lt;0.001</td>
<td>0.59 - 0.74</td>
</tr>
<tr>
<td>Summer 'climate' last year</td>
<td>-0.04 (0.01)</td>
<td>-2.98</td>
<td>0.003</td>
<td>-0.06 - -0.01</td>
</tr>
<tr>
<td>Winter 'climate' last year</td>
<td>-0.01 (0.01)</td>
<td>-0.45</td>
<td>0.654</td>
<td>-0.03 - 0.02</td>
</tr>
<tr>
<td>Summer 'water quality' last year</td>
<td>-0.03 (0.02)</td>
<td>-1.34</td>
<td>0.180</td>
<td>-0.07 - 0.01</td>
</tr>
<tr>
<td>Winter 'water quality' last year</td>
<td>-0.02 (0.02)</td>
<td>-0.68</td>
<td>0.500</td>
<td>-0.06 - 0.03</td>
</tr>
</tbody>
</table>

### b)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate (SE)</th>
<th>t</th>
<th>p</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.69 (0.04)</td>
<td>17.32</td>
<td>&lt;0.001</td>
<td>0.61 - 0.76</td>
</tr>
<tr>
<td>Summer 'climate' last year</td>
<td>-0.06 (0.01)</td>
<td>-4.82</td>
<td>&lt;0.001</td>
<td>-0.08 - -0.03</td>
</tr>
<tr>
<td>Winter 'climate' last year</td>
<td>-0.02 (0.01)</td>
<td>-1.37</td>
<td>0.173</td>
<td>-0.01 - 0.04</td>
</tr>
<tr>
<td>Summer 'water quality' last year</td>
<td>-0.04 (0.02)</td>
<td>-1.91</td>
<td>0.056</td>
<td>-0.08 - 0.00</td>
</tr>
<tr>
<td>Winter 'water quality' last year</td>
<td>0.03 (0.02)</td>
<td>1.17</td>
<td>0.243</td>
<td>-0.02 - 0.07</td>
</tr>
</tbody>
</table>
Table 5. Values of raw climatic variables (monthly average) at 5, 25, 75 and 95 percentiles of Principal Component scores derived from a Principal Component Analysis of summer climatic variables relevant to the Wye river system (see Table 3 for loadings).

<table>
<thead>
<tr>
<th>Percentiles</th>
<th>PC1 summer scores</th>
<th>Rainfall (mm)</th>
<th>Sun (hours)</th>
<th>NAO</th>
<th>Discharge (m³/s)</th>
<th>Tmax °C</th>
<th>Tmin °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>5%</td>
<td>-1.469</td>
<td>62.4</td>
<td>173.3</td>
<td>-0.131</td>
<td>0.346</td>
<td>18.2</td>
<td>9.3</td>
</tr>
<tr>
<td>25%</td>
<td>-0.828</td>
<td>48.2</td>
<td>169.8</td>
<td>-0.588</td>
<td>0.264</td>
<td>18.6</td>
<td>10.1</td>
</tr>
<tr>
<td>75%</td>
<td>0.761</td>
<td>38.2</td>
<td>202.1</td>
<td>-0.222</td>
<td>0.130</td>
<td>18.9</td>
<td>9.0</td>
</tr>
<tr>
<td>95%</td>
<td>1.762</td>
<td>36.0</td>
<td>213.6</td>
<td>0.340</td>
<td>0.124</td>
<td>20.5</td>
<td>10.0</td>
</tr>
</tbody>
</table>
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)

<table>
<thead>
<tr>
<th>Site</th>
<th>Site Coordinates</th>
<th>Slope b ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Itchen, Eastleigh¹ (SU 454157)</td>
<td>0.76 ± 0.01</td>
<td></td>
</tr>
<tr>
<td>Bere, Dorset¹ (SY 859 919)</td>
<td>0.68 ± 0.02</td>
<td></td>
</tr>
<tr>
<td>Avon, Amesbury¹ (SU 151 413)</td>
<td>0.51 ± 0.02</td>
<td></td>
</tr>
<tr>
<td>Frome² (SY868861)</td>
<td>0.94 ± 0.02</td>
<td></td>
</tr>
<tr>
<td>Lambourne² (SU452693)</td>
<td>0.62 ± 0.02</td>
<td></td>
</tr>
<tr>
<td>Winterbourne² (SU453694)</td>
<td>0.48 ± 0.02</td>
<td></td>
</tr>
<tr>
<td>Tadnol Brook² (SY800874)</td>
<td>0.74 ± 0.03</td>
<td></td>
</tr>
<tr>
<td>Moorland stream (CI6; SN772 556)³</td>
<td>0.94 ± 0.04</td>
<td></td>
</tr>
<tr>
<td>Moorland/forest stream (AT; SN804 538)³</td>
<td>0.97 ± 0.04</td>
<td></td>
</tr>
<tr>
<td>Forest stream (L11; SN809 529)³</td>
<td>0.78 ± 0.09</td>
<td></td>
</tr>
<tr>
<td>Plynlimon forest stream (Hafren; SN8487)⁴</td>
<td>0.66-0.73</td>
<td></td>
</tr>
<tr>
<td>Plynlimon forest stream (Hore; SN8388)⁴</td>
<td>0.51-0.71</td>
<td></td>
</tr>
<tr>
<td>Wye catchment, wooded headwaters⁵</td>
<td>0.72 ± 0.04</td>
<td></td>
</tr>
<tr>
<td>Wye catchment, main tributaries⁵</td>
<td>0.94 ± 0.07</td>
<td></td>
</tr>
</tbody>
</table>
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 ±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: \(y = 0.0413x - 70.759\); \(r^2 = 0.38\)), summer (b: \(y = 0.0339x - 50.414\); \(r^2 = 0.1164\)) and winter (c: \(y = 0.0504x - 93.782\); \(r^2 = 0.1411\)) 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) (\(y = 0.0732x - 145.95\); \(r^2 = 0.4264\)).

**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 100m\(^2\) reach averaged (mean ± 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.
<table>
<thead>
<tr>
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<tbody>
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<tr>
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Figure 2
Figure 3:
c) Winter temperature

- Temperatures range from approximately 4°C to 9°C.
- A clear upward trend is observed from 1980 to 2005.

b) Summer temperature

- Temperatures range from approximately 12°C to 20°C.
- A clear upward trend is observed from 1980 to 2005.

d) Winter temperature residual after NAO

- Temperatures range from approximately -2°C to 2°C.
- A clear upward trend is observed from 1980 to 2005.
Figure 4

a) Summer

b) Winter
Figure 5

(a) Index of antecedent summer climate vs. juvenile salmon density / 100m²

(b) Index of antecedent summer climate vs. juvenile trout density / 100m²