



Evaluating climatic effects on aquatic invertebrates, Phase II: review, comparisons between regions and methodological considerations

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Miranda Kavanagh **Director of Evidence**

Executive summary

Rivers are sensitive to climate change through effects on discharge and temperature, but the consequences for river organisms are poorly understood. This report is the second phase of an investigation of potential climate-change effects on invertebrates in British rivers with the overall objective, set by the Environment Agency, of informing 'broad-scale predictions'. This required a continuation of Phase I analysis of chalk streams, a review of available literature and an assessment of comparative trends from contrasting upland and lowland rivers. The specific aims were to:

- outline available literature on sensitivity among different groups of river invertebrates, and possible pathways of effect;
- appraise further recent climatic effects on lowland chalk streams using variance partitioning at specific sites unconfounded by trends in water quality;
- compare trends in contrasting lowland chalk streams with upland Welsh hill streams (Llyn Brianne);
- assess the effects of data quality (i.e. family-level identification and semiquantitative abundance) on the detection of climate-change effects using Environment Agency data;
- assess whether the changing geographical distribution of selected invertebrate families across England and Wales, as recorded by the Environment Agency, might indicate climate-change effects or sensitivity.

Recent published literature confirms that climate change now affects freshwater invertebrates in Europe (UK, France, central and northern Europe, alpine environments), North America, Australia and New Zealand. Climate change also appears to affect resources important to invertebrates, such as leaf-litter and macrophytes. Both discharge and thermal changes are involved. For discharge, widely used Environment Agency metrics such as LIFE scores are available for use as potential climate-change indicators. For temperature, thermal indices are unavailable. Some common insect groups have more flexible life histories (e.g. some Ephemeroptera) than others (e.g. Plecoptera), implying contrasting, and potentially facultative, responsiveness to climatic change. Plecopterans may be particularly sensitive to warming, and characterise higher-altitude sites. Direct climate-change effects are clearest at sites where other pressures, such as water quality, are absent or well quantified, but interactions with other pressures require fuller examination.

Further analysis here confirmed that water quality best explains recent invertebrate trends at chalk-stream sites in Dorset, Avon and the Bristol Avon. Nevertheless, at specific locations (e.g. Cheriton stream) and in aggregate across sites in the Itchen system, inter-annual flow variations have been sufficient to cause variations in invertebrate composition of c. 20% since 1989 – far larger than any effects of water quality or temperature. These recent inter-annual variations in discharge have also been large by comparison with climate-change projections for southern Britain under UKCIP 09. Simulations suggest that climate-change effects on flow in chalk streams would change invertebrate family composition by <2–3% over the 2020s to 2050s. Nevertheless, flow effects on invertebrates could still occur if climate change augments existing patterns of variability.

Inter-annual discharge variations over recent decades have been similar in upland Welsh streams (385% summer vs. 246% winter) and selected chalk streams (340%

winter vs. 232% summer), although the exact seasonal patterns differ. In neither case have discharge volumes changed progressively through time, but there has been marked inter-annual variability over recent years in the chalk-fed Itchen.

Variations since 1981 in winter mean temperature have been larger in lowland chalk streams (inter-annual range c. 4.9°C) than in upland streams at Llyn Brianne (interannual range 2.7°C), despite significant North Atlantic Oscillation (NAO) effects on the latter and groundwater damping effects on the former. Winter temperatures have increased almost twice as rapidly through time in chalk streams as opposed to upland Welsh streams (gain c. 2.6 vs. 1.4°C), but summer trends have not been statistically significant.

For years with contemporaneous data and at sites unaffected by water quality, invertebrate composition in upland streams tracked temperature, while lowland chalkstream assemblages tracked discharge. Chalk-stream functional composition varied as the richness of both grazers and filter-feeding invertebrates increased at higher flows. Invertebrate abundance declined with temperature in the upland Welsh streams, but could not be assessed in chalk streams due to the type of data available.

Possible explanations for these contrasting ecological responses to climatic variation in upland and lowland streams are that:

- upland stream invertebrates are more sensitive to temperature variations while chalk-stream invertebrates are more sensitive to discharge;
- high winter temperatures in the lowland chalk sites have coincided with increased discharge, which might offset adverse warming effects;
- the quality of data available from chalk streams (family-level with semiquantitative abundances) masks temperature effects.

The first two of these hypotheses require further investigation. The third hypothesis was tested by re-treating long-term Welsh data to show that temperature effects on assemblages would not have been detected using methods similar to Environment Agency monitoring.

At a larger scale, distributional changes across the whole of England and Wales for selected invertebrate families included examples of:

- inter-annual variation without marked increase or decrease (Perlodidae, Nemouridae);
- increase through time (Ephemeridae);
- apparent recent increase accompanied by inter-annual variation (Rhyacophildae, Heptagenidae, Taeniopterygidae);
- apparent substantial decrease (Cordulegastridae).

Some of these national changes are consistent with trends in discharge and water quality effects, but the data also reveal some reduction in the prevalence of cooler-water families typical in upland, western regions between the 1990s and present day (Cordulegastridae, Nemouridae, Taeniopterygidae). These distributional effects require further quantitative analysis, but care will be needed to separate potentially confounding causes of change.

From all the foregoing investigations, we conclude that several lines of emerging evidence are consistent with the influence of climate change or inter-annual climatic variation on river invertebrates in England and Wales. They include changes in abundance, composition, distribution and functional character, with temperature effects most implicated in upland locations and inter-annual discharge variations implicated in some chalk streams. However, improving water quality might have masked or offset climate-change effects in some lowland chalk streams despite substantial temperature gain. This effect may be widespread in other river types where water quality has improved. One important caveat is that the type of data available from most Environment Agency monitoring – involving family-level identification – might also have insufficient resolution to detect some climate-change effects.

Despite available evidence, there are major gaps in evidence on the ecological mechanisms involved in climate-change effects on river invertebrates, on the consequences for river ecosystem function, on the consequences for invertebrate predators such as salmonids, on interaction with other stressors, on the best adaptive responses, and on factors affecting resistance and resilience to climate-change effects.

We now recommend:

- That further assessment be made of combined temperature and discharge effects on aquatic invertebrates, and of how climate change will augment existing patterns of inter-annual variability.
- That the Environment Agency increases support for invertebrate monitoring projects aimed at detecting climate-change effects on rivers. Important effects will go undetected without species-level identification.
- That research effort should be given to understanding better the mechanisms, ecological consequences and functional consequences of climate-change effects on river invertebrates. Possible approaches include analysis of long-term or distributional data, experiments, and the use of climate-analogues in space and time The consequences of climate change for ecosystem function will be highlighted by growing interest in ecosystem services, but these effects will not be captured by current Environment Agency monitoring.
- That more effort is expended on understanding interactions between climate-change effects and other stressors on the UK river environment (e.g. abstraction, eutrophication, sediment mobilisation, acidification, flood-risk management, poor habitat quality).
- That the significance of these results should be considered by the Environment Agency and its sister agencies with respect to developing adaptive responses to climate change in the river and riparian environment.
- That factors affecting resistance and resilience to climate change be investigated more fully.

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1 General introduction

Growing evidence suggests that rivers and streams are highly sensitive to climate change because their temperatures track atmospheric trends and because their flow regimes depend on precipitation pattern. River organisms and processes are likely to be influenced strongly by the resulting changes, and indications of ecological effects in Europe are now accumulating (Daufresne *et al.* 2004, 2007, Bonada *et al.* 2007). In upland Britain, river temperatures have increased over the last two to three decades, with invertebrate composition and abundance responding to these and other climatic effects (Bradley and Ormerod 2001, Durance and Ormerod 2007). By contrast, recent warming in some English chalk streams has been accompanied by gains, rather than losses, among sensitive invertebrate families (Durance and Ormerod 2009). Trends in this case were best explained by improving water quality, but changes in flow were implicated at some sites. This and previous evidence suggests that any climate-driven changes in discharge could be as important as temperature in affecting chalk-stream species. However, these and other ecological effects of climate on rivers are still poorly understood and require further investigation.

The Environment Agency and Wessex Water commissioned studies of climate-change effects on rivers during 2007 in a first phase of work focused specifically on chalk streams (Durance and Ormerod 2008). This report on the second phase of this work continues this theme, but in addition the Environment Agency requested that the aims should be widened. Specifically, it asked that climate sensitivity be reviewed among those river invertebrates that constitute significant prey to fish so that broad-scale predictions could be made about possible changes in their composition, range, phenology and abundance. This required not only a review of available literature, but also a comparative assessment of trends in available site-specific and broad-scale data. Since some of the latter are from the Environment Agency, and involve family-level identification with semi-quantitative abundances, some specific assessment was also required of how well such data might reflect climatic effects. Temperature or flow tolerance can vary between species within families, and hence family-level data could mask species-level trends (e.g. Hildrew and Edington 1979).

The specific aims were:

- to review, in outline, available literature on sensitivity among different groups of river invertebrates, and possible pathways of effect;
- to appraise further the recent climatic effects on lowland chalk streams using variance partitioning, particularly at specific sites free of confounding trends in water quality, and where discharge effects might be more likely;
- to compare trends in these lowland chalk stream with upland Welsh hill streams (Llyn Brianne) thereby providing a contrast between systems differing in taxonomic composition, thermal mass, groundwater contribution, hydrological regimes and sensitivity to the North Atlantic Oscillation;
- to assess the possible effects of data quality notably family-level identification and semi-quantitative abundance – on the detection of climatic effects using Environment Agency data;
- to assess whether the changing geographical distribution of selected invertebrate families across England and Wales, as recorded by the Environment Agency, might indicate climatic effects or sensitivity.

2 Literature review: climatechange effects on rivers and their invertebrates

2.1 Introduction

For reasons expanded elsewhere in these two reports (see Phase I), rivers are sensitive to climate-change effects because:

- their temperatures track air temperature closely (Caissie 2006, Durance and Ormerod 2007), potentially affecting ectothermic river organisms and key physico-chemical conditions (e.g. oxygen concentrations) or processes;
- climatic effects on precipitation will increasingly affect river hydrology and hydraulics (Wilby 2006);
- river conditions and processes are linked closely to those affecting their riparian zones and catchments (White *et al.* 1998);
- rivers respond to other large-scale climatic phenomena such as El Niño or the North Atlantic Oscillation (NAO) (Elliott *et al.* 2000, Bradley and Ormerod 2001, Blenckner and Hillebrand 2002, Briers *et al.* 2004, Gilbert *et al.* 2008);
- climate change potentially interacts with other aspects of global change such as eutrophication, organic pollution, acidification and exotic species' invasion (Root *et al.* 2003, Evans 2005, Daufresne and Boet 2007, Durance and Ormerod 2007, 2009, Viney *et al.* 2007).

A literature review for the Environment Agency on some of these climatic effects on freshwaters has been produced previously (Conlan *et al.* 2005), outlining some of the direct and indirect pathways through which rivers and river organisms could be affected by changing discharge and temperature (Figure 2.1). A range of other published reviews concerning general aspects of climatic effects on rivers is also available, for example on:

- effects on river temperature, and its general ecological consequences (Caissie 2006, Dallas 2008);
- general effects of floods and droughts on stream organisms (Lake 2000);
- climate-change effects on freshwater biodiversity (Heino et al. 2009).

In addition, other reviews have speculated about possible ecological effects of climate change on rivers – often in the absence of real data and evidence (Grimm *et al.* 1997, Hauer *et al.* 1997, Mulholland *et al.* 1997). Some of these suggest that climate-change effects may be less important than other well-known pressures on river ecosystems, but this view is increasingly dated (Malmqvist and Rundle 2002). Others suggest that a predicted increase in the severity and frequency of disturbances with global climate change requires a comprehensive and improved understanding of the ecology of running water organisms (Lake 2000).

This contribution concentrates, therefore, directly on the observed effects of climate change on river invertebrates, thereby satisfying the sponsors' requirement to inform 'broad-scale predictions' about climate-change effects on important river-fly groups.

Resource constraints precluded an exhaustive review, and in addition primary literature on climate-change effects on individual groups of invertebrates is still limited in volume. The intention was, nevertheless, to produce an annotated bibliography that outlines:

- recent evidence for general climate-change effects on river invertebrates;
- possible pathways involving temperature;
- possible pathways involving discharge.

Methods: literature identification and collection

Initial literature searches for papers that potentially identified macroinvertebrate responses to climate, mediated by temperature or discharge effects investigated published papers containing the key words 'invertebrate' or 'macroinvertebrate' and terms associated with (i) climate, (ii) temperature ('temperature' or 'thermal') or (iii) discharge ('discharge', 'flow', 'flood' or 'drought') listed on the ISI[®] database between 1980 and 2007 (Figure 2.2). A similar search using 'insect' as a keyword yielded and additional 145 journal articles. A further search for papers with specific reference to 'Ephemeroptera', Plecoptera or 'Trichoptera' resulted in a further 197 papers. From this total of 655 papers, key items were identified that may provide details on macroinvertebrate response to temperature or flow effects.



Figure 2.1 Possible broad-scale effects on river organisms through direct changes in precipitation or discharge, or indirect effects, for example through interactions with water quality (after Conlan *et al.* 2005).



Figure 2.2 Published papers with key words 'invertebrate' or 'macroinvertebrate' and terms associated with (i) temperature ('temperature' or 'thermal', n = 203) or (ii) discharge ('discharge', 'flow', 'flood' or 'drought', n = 100) listed on the ISI[®] database between 1980 and 2007.

2.2 Evidence of general climate-change effects on river invertebrates

Although there has been long-standing speculation about the possible effects of climate change on river invertebrates, good quality data are only now emerging from studies at suitable spatial or temporal scales (Beche and Resh 2007). The methods have included long-term studies (Durance and Ormerod 2007), the use of analogue effects provided by natural climatic variability between regions (Bonada *et al.* 2007) or times (Bradley and Ormerod 2001), experiments (Hogg and Williams 1996) and modelling (Buzby and Perry 2000). The available results suggest the following:

- Variations and temporal trends in precipitation can shift invertebrate communities in drier regions between taxa adapted to low flow to those typical of wetter, high-flow conditions. These effects in some locations have led to sustained compositional changes, with small streams particularly at risk (Beche and Resh 2007, Chessman in press). Long-term investigations of this type are concentrated in Mediterranean regions, and there are no published data from the drier UK regions.
- Large-scale, and quasi-natural climatic variations (e.g. El Niňo Southern Oscillation, North Atlantic Oscillation) can affect the stability and persistence (i.e. year-to-year similarity) of invertebrate assemblages, with parallel results observed on at least two continents (Bradley and Ormerod 2001, Beche and Resh 2007). In some cases, discharge variations are dominant in these effects, but in the UK they also include stream temperature and hydrochemistry chemistry (Bradley and Ormerod 2001).
- Inter-region comparisons with areas that mimic future climates in temperate areas have allowed some assessment of the ecological effects of increasingly seasonal discharge, torrential floods and severe droughts. These comparisons suggest that climate change will affect the taxonomic composition of invertebrates far more than the ecological traits they

represent – i.e. the broad array of invertebrate types present (Bonada *et al.* 2007). Climate change is therefore expected to have strong implications for local biodiversity conservation because of its emphasis on species composition. Regions with variable climates similar to those expected in future in the UK are, nevertheless, characterised by macroinvertebrates with good dispersion and colonisation capabilities suggesting that they may move northwards to replace displaced cooler water species. This is clearly speculative and requires assessment by longer-term monitoring.

- Long-term studies of effects on the abundance and community composition of invertebrates typical of cooler-water headwaters indicate losses among the latter, apparent in headwaters in Wales (Durance and Ormerod 2007) and the upper Rhone (Daufresne *et al.* 2004) where temperatures have increased. In the latter case, changes have been linked with higher temperatures, decreased oxygen content and extreme hydroclimatic events (e.g. the 2003 heatwave, Daufresne *et al.* 2007). Similar effects have also been observed on other continents, most recently Australia (Chessman in press). They are also matched by long-term shifts among European lake macroinvertebrates where temperatures have increased (Burgmer *et al.* 2007).
- Increasing risks of extinction to local, aquatic invertebrates in specific highaltitude environments, for example those affected by meltwater (Brown *et al.* 2007). Such highly specialised cool-water environments are scarcer in Britain, but there are, nevertheless, some specific northern and higheraltitude taxa that may be at risk.
- Potential subtle effects of combined long-term changes of temperature and discharge, for example on invertebrate emergence patterns (Harper and Peckarsky 2006).
- Climate change influences key food resources to invertebrates, such as the processing rates and standing stocks of coarse organic matter in leaf packs (Buzby and Perry 2000). Discharge variations might also affect invertebrates by changing stream macrophyte communities (e.g. Westwood *et al.* 2006), by affecting stream nutrient availability (Hong *et al.* 2005), or by altering the availability of stream habitats (Cattaneo *et al.* 2004), but these effects are poorly understood.
- Observational and experimental data suggest that climate-change effects are often most apparent explicitly at sites where other pressures, such as water quality, are absent or well understood (e.g. Daufresne and Boet 2007, Dewson *et al.* 2007, Durance and Ormerod 2007, 2009, Viney *et al.* 2007). However, interactions with other pressures require fuller examination, and could be among the most important effects. In general, such interactions are likely to be negative, for example through increased bacterial contamination and reduced pollutant dilution at low flow (Caruso 2001, 2002). However, positive interactions have also occurred, for example where drought effects reduced the effects of acidification on some southern English streams (Woodward *et al.* 2002).

In combination, these studies support the assertion that river invertebrates are sensitive to climate change and variation, with evidence of effects on composition, abundance, phenology, range changes, extinction risk and changing resource availability. There are suggestions that certain river types – such as headwaters – might be most at risk, although the basis for this suggestion is so far limited. Processes responsible have included combinations of temperature, discharge and interactions

with chemistry, although studies that allow an assessment of which of these is most important, and under which circumstances, are still few.

2.3 Temperature

As indicated in Figure 2.1, temperature effects on rivers can arise in a variety of ways, for example involving absolute temperature magnitude, changes in range, accumulated degrees, changes in seasonality and alterations in freeze/thaw patterns. There are consequences for other physical factors dependent on temperature, such as oxygen concentrations. Effects on organisms can arise directly through their metabolic rate and energy requirement, because their upper lethal limits are exceeded, or because their life cycle and phenology is altered (development times, emergence, diapause, voltinism...). Indirect effects are also likely through changing resource use and availability, or the effects of altered energy demands from predators. As a result, there are potential large consequences for distribution, abundance, inter-specific interactions, community composition, altitudinal and geographic range. Well-established knowledge shows, for example, how variations in thermal tolerance and feeding activity with invertebrate families is key to understanding altitudinal downstream sequences between species (Hildrew and Edington 1979. Temperature is among the array of downstream trends that affect overall diversity in rivers, as well as the progressive shift in invertebrates from cooler-water Plecoptera and Ephemeroptera to warmer-water molluscs, crustaceans, Hemiptera and other typical lowland taxa. Note, also, that for insects, there are potential thermal effects on the adult (flying) stages as well as the aquatic stages.

Direct effects

Recent additional evidence about temperature effects on river invertebrates includes the following:

- High-altitude sites are often occupied by cool-water specialists, adapted for growth at low temperature, and there are risks that these groups face local extinction (Winterbourn *et al.* 2008). Evidence of such local extinction is already available from Wales from the flatworm *Crenobia alpina* (I. Durance and S.J. Ormerod, unpublished data). These losses will occur in spite of colonisation from species at lower altitudes adapted to higher temperatures (Jacobsen *et al.* 1997, Oertli *et al.* 2008). In Britain, systematic long-term data from any such sensitive habitats are few, and trends will reflect the contrasting balance between species loss by local extinction and gain through changing range. Indications over the last 25 years are that losses in cooler habitats outweigh gains (Durance and Ormerod 2007).
- Indications that there are variations among insect species in life-cycle flexibility in space (i.e. between climate zones) and times (i.e. between warm and cooler periods), with potential consequences for development times, hatching or flight periods and range (Braune *et al.* 2008). Some common insect groups have more flexible life histories (e.g. some Ephemeroptera) than others (e.g. Plecoptera), implying contrasting, and potentially facultative, responsiveness to climatic change (Robinson *et al.* 2000, Briers *et al.* 2004). Plecopterans, with their cool-water tolerance, may be particularly sensitive to warming effects, and generally characterise higher-altitude sites (Prenda &Gullardo-Mayenco. 1999). Timing hatching or emergence events to maintain synchronicity with ideal conditions, derived ultimately through evolutionary processes, may be important

(Fureder *et al.* 2005). However, the consequences of any of these effects for community composition, community change or resilience are poorly understood.

- There is increasing recognition of some of the factors affecting variation in the temperatures of rivers, and their associated habitats, at a range of scales (e.g. Hawkins *et al.* 1997, Arscott *et al.* 2001). Lowland rivers, floodplain rivers, and those characterised by large variations in local hydromorphology, variations in water residence time and connectivity among micro-habitats, appear to have greatest thermal heterogeneity, implying wider opportunities for organisms of varying thermal tolerance. In contrast, upland river habitats might provide more limited heterogeneity, and hence more limited niche-space, although consequences of such effects for invertebrates are poorly understood and few hypotheses have been tested on real data.
- Direct experimental evidence from heating in stream channels shows that warming can decrease total invertebrate densities, advance insect emergence, alter growth rates and times of breeding in aquatic crustaceans, reduce size at maturity for some taxa and even alter sex ratios in others. Experiments of this type are scarce globally, and there are none in Britain.

2.4 Discharge

As indicated in Figure 2.1, any discharge variations linked to climate change would affect a wide range of key ecological characteristics in rivers including hydraulics, the shape and timing of the flood hydrograph, velocity profiles, wetted perimeter, habitat physiography, processes of erosion, sediment transport and deposition, and the dilution of both natural solutes and pollutants. Effects might arise not only through changes in average flows but also through the frequency and magnitude of extreme events of both high and low flow.

Extensive evidence is available to illustrate qualitatively how variations in discharge might affect organisms, and the Environment Agency already makes extensive use of this information through metrics such as LIFE scores (e.g. Monk *et al.* 2008). These and other dimensions form part of the growing subject area of ecohydrology, served by dedicated journals. However, quantitative examples of direct interactions between climatic variation and discharge effects on river organisms are fewer. Recent examples include:

• Evidence of both nationwide and region-specific variations in LIFE scores in English rivers following major drought events (1990–1992 and 1996–1997), with reductions followed by subsequent recovery (Monk *et al.* 2008). Invertebrate response to high flow in 1994 and 1995 was also apparent, although less marked. Two implications of these results are that low-flow effects on invertebrates are stronger than high-flow events, but recovery appears to be rapid. It is unclear how more prolonged 'press' effects of low flows, across several years, might result in longer-term changes since these have been assessed far less frequently (Humphries and Baldwin 2003). There is some evidence of these progressive effects in Mediterranean streams in California (Beche *et al.* 2006).

- Factors rendering rivers most prone to drought effects on invertebrates are also incompletely understood. Two possible approaches to better understand such effects might involve:
 - investigations to link variations in assemblages to hydromorphological aspects of streams, such as flow regimes, as a possible means of understanding discharge effects (Monk *et al.* 2006);
 - assessing variations in the traits of organisms that might make some streams more susceptible. There is some evidence that drought-prone streams are characterised by invertebrates with certain life-history traits (small size, multivoltinism, diapause, ovoviviparity) that contrast with those in stable, favourable environments (large body size, semivoltinism, isolated eggs etc.) (Diaz et al. 2008). Similar trait-based variations also occur between dry and wet years, when taxa can switch between those with traits conferring resistance or resilience to drving (e.g. desiccation resistance, aerial respiration) to those conferring resistance or resilience to floods (e.g. flattened body shape, drift dispersal; Beche & Resh 2007). Trait-based assessments of sensitivity to climatic variations could be more meaningful than comparisons between insect orders, since life-history strategies vary often within taxa, while whole orders (e.g. Ephemeroptera, Plecoptera and Trichoptera) often vary similarly with flow-related effects (e.g. Bonada et al. 2007, Dewson et al. 2007, Chaves et al. 2008). Trait-based approaches also allow some assessment of the possible mechanisms through which flow effects arise (Wagner and Schmidt 2004) Fenoglio et al. 2007).
- Long-term investigations elsewhere suggest that drought effects and mechanisms also vary between biomes or climatic zones. For example, in Mediterranean climates floods rendered some invertebrates more vulnerable to predation than low- flow conditions by reducing algal food abundance (Power *et al.* 2008). In contrast, temperate Canadian or New Zealand streams responded similarly to those in the UK, with reduced abundances of Ephemeroptera, Plecoptera and Trichoptera (EPT) after drought (Caruso 2002, Gilbert *et al.* 2008). While the latter of these two studies illustrates that different orders respond similarly to drought effects, the former illustrates some of the complex pathways through which flow variation can affect invertebrates under some circumstances.
- Inter-biome comparisons within Europe also illustrate how hydrological variations have major effects on invertebrates through trophic interactions. In Atlantic temperate streams draining woodland, the standing crop and retention of benthic detritus is large and important to invertebrates, but also is affected by flood and drought effects. In contrast, Mediterranean streams have higher chlorophyll concentrations so that stream grazers are more prevalent through their dependence on algae (Sabater *et al.* 2008).
- There are examples where discharge variations due to regulation reducing or increasing flows have affected invertebrate densities, but these are underused as experimental methods of assessing potential climate-change effects on invertebrates (Fjellheim *et al.* 1993).

3 Climatic effects on chalk streams: further analysis

3.1 Introduction

Phase I of this study reported on the possible results of climatically mediated effects on chalk stream invertebrates (Durance and Ormerod 2008, 2009). The major findings were that temperatures have increased in chalk streams over recent decades, consistent with climate change, but effects on invertebrates have been confounded by improving water quality and varying flow over the study period.

There were several uncertainties about these results, as reported. (i) The use of simple regression might not adequately capture the relative effects of different explanatory variables (water quality, discharge, temperature...) on invertebrates. (ii) Gaps in data availability meant that aggregate trends were analysed across sites, rather than within sites. (iii) Most important of all, more detailed analysis was required at sites where water quality had been constant through time to assess any climatically mediated effects at sites free of possible confounding effects related to water quality.

One of the key aims of this report, therefore, was to address these uncertainties by reappraising the Environment Agency's data from chalk streams using a different analytical method (various partitioning) and by assessing trends at individual sites with long data-runs where water quality changes could be avoided. This analysis sought to confirm the initial conclusions that (i) improving water quality explained trends in among invertebrates in some chalk-stream sites better than did increasing temperature and (ii) where water quality trends were smaller, discharge variations explained more variation in chalk-stream invertebrates than did temperature (Durance and Ormerod 2008).

The initial scope for the project included an intention to project future warming effects on chalk streams, but since no clear warming effects on invertebrates in these streams have so far been detected using Environment Agency data, this aim was not pursued.

3.2 Methods

Full details of site selection are given in the Phase I report (Durance and Ormerod 2008). Briefly, chalk-fed or surface-fed streams with long-term invertebrate data in southern England (Dorset, Avon, Hampshire and Devon) were drawn from the Environment Agency 'BIOSYS' database, with sites mostly from the Dart, Teign, Avill, Bristol Avon, Frome, Piddle, Wylye, Test and Itchen. Prior to any of the following analyses, sites were divided by classification into groups with similar composition. Two major chalk-stream groups were: chalk-fed rivers in Dorset and Avon, and the Bristol Avon (Group 1; n = 19 sites) and chalk-fed streams in Hampshire (Group 2; n = 10).

To assess trends through time in invertebrate assemblages in Groups 1 and 2, Detrended Correspondence Analysis (DCA) scores were plotted through time, and hierarchical variance partitioning was used to assess the relative effects of temperature, discharge and water quality on invertebrate composition in spring or autumn. In this method, all possible permutations of regressions on the predictor variables (separately and in combination) are calculated to identify those predictors that are highly, independently correlated with the dependent variable. This procedure is intended to overcome problems of multicollinearity, spurious causality and model specificity or over-fitting in multivariate regression. While causality cannot be demonstrated over the spatio-temporal scales involved in regional climate-change effects, this approach is considered less likely to lead to spurious deductions because all potentially important predictors are considered concurrently (Chevan and Sutherland 1991, MacNally 1996).

The analysis used R version 2.7.1 (R Development Core Team 2008) and the contributed package hier.part (Walsh and MacNally 2008) to relate invertebrate assemblages in spring to temperature, water quality and standardised discharge in the preceding winter and the previous summer. Similarly, autumn invertebrate data were related to the preceding summer and previous winter. Both cases allowed the detection of antecedent effects from the previous season as well as annual effects over typical, univoltine, life cycles.

To assess trends and apparent effects at individual sites, analysis focused on the River Wylye in the Avon catchment (Dorset; $51^{\circ}06$ 'N $1^{\circ}49$ 'W) and Cheriton stream in the Itchen catchment (Hampshire: $50^{\circ}56$ 'N $1^{\circ}21$ 'W). Each was selected as the site with the most complete data-run from each of two main site-groups (Groups 1 and 2). Each was also directly adjacent to specific monitoring points for water quality and discharge, and each stream had generally similar chemistry (Table 3.1). Specific DCA was carried out on samples from each of these two streams, based on 42 invertebrate taxa in the Wylye (n = 26 samples, 1991–2006) and 45 in the Cheriton (n = 31 samples, 1989–2006), and hierarchical variance partitioning was used as before to assess the most likely influences on changing composition.

Table 3.1 Water quality indicators in two chalk streams in southern England selected for site-specific assessment of long-term change. The values are means (\pm SD) calculated from monthly data during 1992–2006.

Water quality variable	Cheriton	Wylye
Total oxidised nitrogen (mg/l)	5.9 ± 0.7	6.1 ± 0.7
Ammonia (mg/l)	0.04 ± 0.02	0.06 ± 0.06
BOD (mg/l)	1.25 ± 0.38	1.40 ± 0.34
Orthophosphate (mg/l)	0.04 ± 0.04	0.27 ± 0.14

3.3 Results

As in the initial analysis using regression (see Phase I report), water quality explained larger proportions of variance through time in invertebrate composition at Group 1 sites than did temperature or discharge (Table 3.2). Similarly, at Group 2 sites, variations in discharge during the antecedent winter or summer explained more variation in invertebrates than did either water quality or temperature, with effects most apparent in spring samples.

Site-specific trends

Consistent with trends in the larger site groups, DCA scores declined through time at individual sites both in the Wylye ($r^2 = 52.8\%$, $F_{1, 21} = 22.4$, P<0.0001) and the Cheriton ($r^2 = 26.1\%$, $F_{1, 25} = 8.5$, P<0.01). Major sources of variation were also similar. In the Wylye (Group 1), water quality in winter and summer explained most variation in assemblage composition. In the Cheriton (Group 2), most trends in invertebrate assemblages were explained by discharge. As in the initial analysis from Phase I,

temperature effects on organisms were apparently significant, but in the opposite direction to those expected from adverse impacts since sites gained taxa typical of faster flows and better oxygenated conditions (Table 3.3).

Based on the outcomes of variance partitioning, simple regression models produced for the Wylye indicate that changes in water quality, for instance a decrease in BOD of c. 0.2–0.4 mg/l would be sufficient to shift invertebrate assemblages by 0.40 SD in spring and 0.64 SD in summer. This represents a change in typical composition of around 10–16%, and a gain in pollution-sensitive families (Table 3.4). On the same basis for the Cheriton, the inter-annual range of discharge over the course of the study of 4 to 12 m³/s at the adjacent Highbridge gauging station could change DCA scores by 0.79 SD, a turnover of up to c. 20% in taxonomic composition. As in the Phase I results, low flow effects altered assemblage composition towards taxa typical of low flows, while higher flows increased taxa typical of well-oxygenated conditions and fast flows.

Table 3.2 Variables explaining most variation in invertebrate assemblage composition (as DCA1 scores) through time in two groups of southern English chalk streams according to hierarchical variation partitioning of R-square. Predictors with significant total contribution (R-square) are in bold text. Group 1 sites were chalk-fed streams in Dorset and Avon, and the Bristol Avon (n = 19 sites). Group 2 were chalk-fed streams in Hampshire (n = 10). See Phase I report for details (Durance and Ormerod 2008).

Group and season	Independent variables	Independent contribution	Joint contribution	R-square	Р
Group 1	Winter water quality	0.328	0.195	0.523	0.002
Spring	Winter temperature	0.188	0.304	0.492	0.005
(Dorset &	Summer water quality	0.111	0.149	0.261	0.052
Bristol	Summer temperature	0.103	0.134	0.238	0.065
Avon)	Winter discharge	0.059	0.124	0.183	0.111
	Summer discharge			0.064	0.359
Group 1	Winter water quality	0.135	0.174	0.309	0.031
Autumn	Summer water quality	0.123	0.151	0.274	0.045
	Winter temperature	0.100	0.063	0.163	0.135
	Summer discharge	0.089	0.035	0.124	0.198
	Winter discharge			0.010	0.721
	Summer temperature			0.000	0.979
Group 2	Winter discharge	0.171	0.262	0.433	0.008
Spring	Winter water quality	0.161	0.276	0.437	0.007
(Hants	Summer discharge	0.150	0.137	0.287	0.032
chalk	Winter temperature	0.125	0.220	0.344	0.017
streams)	Summer temperature			0.000	0.955
	Summer water quality			0.006	0.785
Group 2	Summer discharge	0.306	0.133	0.439	0.004
Autumn	Winter discharge	0.241	0.296	0.536	0.001
	Winter temperature	0.106	0.160	0.266	0.028
	Summer temperature	0.060	0.027	0.087	0.235
	Winter water quality			0.081	0.303
	Summer water quality			0.001	0.898

Table 3.3 Variables explaining most variation in invertebrate assemblage composition (as DCA1 scores) through time in two specific southern English chalk streams, the Wylye (from site Group 1) and Cheriton (from site Group 2), according to hierarchical variation partitioning of R-square. Predictors with significant total contribution (R-square) are in bold text.

Stream and season	Independent variables	Independent contribution	Joint contribution	R-square	Ρ
Wylye	Summer water quality	0.443	0.265	0.708	0.002
Spring	Summer temperature	0.184	0.276	0.461	0.031
	Winter water quality	0.172	0.236	0.408	0.047
	Winter temperature	0.137	0.232	0.369	0.063
	Winter discharge	0.026	0.024	0.050	0.534
	Summer discharge			0.011	0.777
Wylye	Summer water quality	0.426	0.199	0.625	0.002
Autumn	Summer temperature	0.152	0.129	0.281	0.076
	Winter water quality	0.086	0.051	0.138	0.235
	Winter temperature	0.071	0.116	0.187	0.160
	Summer discharge			0.000	0.952
	Winter discharge			0.013	0.720
Cheriton	Winter discharge	0.297	0.115	0.412	0.018
Spring	Summer discharge	0.116	0.135	0.250	0.082
	Winter water quality	0.077	0.024	0.101	0.290
	Winter temperature	0.071	0.022	0.093	0.312
	Summer water quality			0.000	0.969
	Summer temperature			0.002	0.897
Cheriton	Summer discharge	0.223	0.267	0.490	0.008
Autumn	Winter discharge	0.134	0.200	0.334	0.039
	Winter water quality	0.128	0.000	0.128	0.231
	Winter temperature	0.109	0.037	0.146	0.198
	Summer water quality	0.045	0.041	0.085	0.332
	Summer temperature			0.001	0.938

Table 3.4 Regression relationships (y = a + bx) relating variations in invertebrate composition (as DCA1 scores) in two southern English chalk streams, the Wylye and Cheriton, to predictor variables over the period 1989–2006. Decreasing DCA scores represent gains in taxa typical of faster flows and well-oxygenated conditions (see Figs 3.8–3.11, Phase I report).

Dependent variable	Independent variable	a (±SE)	b (±SE)	beta	r²	F	Ρ	N of years with data
Wylye spring	Winter water quality	0.588 (0.083)	0.100 (0.043)	0.639	0.41	5.51	0.047	9
Wylye autumn	Summer water quality	0.400 (0.043)	0.156 (0.038)	0.790	0.62	16.4	0.002	11
Cheriton spring	Winter discharge	0.726 (0.152)	-0.070 (0.023)	-0.682	0.46	9.6	0.010	12
Cheriton autumn	Summer discharge	0.991 (0.130)	-0.081 (0.027)	-0.664	0.44	8.7	0.013	12

3.4 Discussion

These results and further analysis using variance partitioning of themes explored initially in Phase I entirely support the conclusions reached at that stage. Of greatest significance to climate-change effects, other sources of variation in chalk streams explain recent trends more powerfully than does temperature change. In particular, recent discharge fluctuations at specific and aggregate sites in the Itchen are sufficient to cause observed variations among taxa typical of faster flows and well-oxygenated conditions, with gains occurring in wetter years.

Considerable evidence about the effects of groundwater level and associated variations in discharge on chalk-stream ecology has accumulated in Britain over the last 30 years (Wright 1992). Marked droughts have included those in 1976, 1988–1992, 1995–1996, 2003–2005/06, although the lengths of dry period have varied, and in some years (e.g. 1995) winter recharge of groundwater levels has moderated effects on discharge. As a consequence, impacts on organisms are more pronounced in some years than others. In general, peak richness in previous chalk-stream data has occurred in or following wetter periods, consistent with the trends recorded here, with recovery from drought usually requiring c. 3 years (Boulton 2003, Wright *et al.* 2004). Mechanisms of effects include variations in velocity, encroachment by marginal vegetation (Wright *et al.* 2004), variation in channel macrophyte cover (particularly *Ranunculus*; Wright *et al.* 2002, Westwood *et al.* 2006) and the removal of lotic taxa during drought by increased sedimentation (Wood and Armitage 1999).

In an interesting parallel to this study, Wood *et al.* (2001) showed that chalk stream invertebrates responded more clearly to hydrological variation than to temperature variation. Recent work in New Zealand streams has revealed that experimental flow reductions affect invertebrates in clean rivers more than under moderate pollution, implying that water quality effects take precedence (Dewson *et al.* 2007). This is consistent with the apparent contrast in water quality and discharge effects on sites in Groups 1 and 2. Further work on the exact mechanisms involved in these effects would

now prove interesting, and the Environment Agency holds some of the key data, for example on macrophytes.

One interesting aspect of the observed discharge variations and effects is that interannual trends have been substantial (230–340%) by comparison with the additional predicted effects of climate change – likely to involve average increases <20% of current mean discharge until at least the 2080s (UKCIP 09 scenarios). On this basis, observed inter-annual variations in invertebrate assemblages are already large by comparison with the likely addition of climatic variation. Much will depend on how future climatic effects augment these current patterns of variability, and on interactions with abstraction.

4 Climatic effects on upland and lowland streams: a comparison

4.1 Introduction

The need in this phase of this project to produce 'broad-scale predictions' about future climatic effects on river ecosystems required some comparative assessment of possible outcomes in contrasting river types. With long-term assessments of climatic effects on British rivers still extremely scarce, the work focused on an explicit upland/lowland comparison – specifically using the lowland chalk streams described above versus Welsh hill streams – on the grounds that:

- long data-runs on stream macroinvertebrates, stream chemistry, stream temperature and discharge were readily available to support such a comparison;
- hill streams, with their smaller thermal mass and smaller influence of groundwater than chalk streams, could be expected to follow air temperature closely;
- hill streams might be expected to be flashy hydrologically, while lowland chalk streams might be less flashy;
- linked to the above point, chalk-stream discharge depends more on current groundwater level than does that of hill streams;
- there is evidence of contrasting effects on these stream types from largescale climatic variation – specifically the North Atlantic Oscillation (NAO) (Durance and Ormerod 2007, cf. Durance and Ormerod 2009);
- upland hill streams and lowland chalk streams have contrasting taxonomic composition respectively of cooler-water species typical of fast flows and taxa with a broader array of flow tolerance;
- hill streams and chalk streams might be at risk from contrasting pressures that might interact with climate (e.g. acidification in the uplands versus abstraction and eutrophication in the lowlands);
- opportunities for climate adaptation differ between upland and lowland settings.

We focused specifically on two individual locations in each of the two regions. The upland study streams – LI6 and LI7 in the Llyn Brianne catchment, in mid Wales, sampled at 310–315 m above sea level have figured in previous climatic studies (Bradley and Ormerod 2001, Durance and Ormerod 2007). The lowland study streams – the Cheriton and Alre in the Itchen catchment in Hampshire (55–60 m above sea level) – also figured in climatic assessments reported in Section 3. Both stream pairs are free as far as possible from other confounding effects such as abstraction, trends in water quality or acidification.

The aims of this case study were:

- to compare observed climatically mediated effects on these two river types for the years which had *contemporaneous environmental data (1981 onwards)*;
- to compare any associated effects on invertebrates, again for years when we had *directly contemporaneous periods (from 1989 onwards)*;
- to consider the reasons for any differences.

It emerged during analysis that one such difference was the quantification and/or taxonomic resolution of the data available respectively from Environment Agency monitoring (family-level with semi-quantitative abundance) and Wales (species-level with direct counts). We examined this possibility directly by recasting the Welsh data to approximate more closely to Environment Agency methods – that is, semi-quantitative data with family-level taxonomy – and reassessed whether climatically mediated trends would still be detectable. Other aspects of data collection were similar, and are outlined below.

4.2 Methods

The upland study area in the central Welsh uplands ($52^{\circ}8'N 3^{\circ}45'W$; Figure 4.1) is maritime and cool-temperate, with mean stream temperatures varying over the range 0–16°C, and mean annual precipitation c. 1900 mm (Weatherley & Ormerod 1990). The underlying rocks are base-poor Ordovician shales and mudstones with peats, peaty gleys and brown podzolic soils, but local calcite veins buffer the two streams studied at circumneutral pH > 6.5 and 15–19 mg/l CaCO₃. In contrast to adjacent streams recovering from acidification, there have been no trends for example in pH. Total oxidised nitrogen is typical for upland streams, and neither ammonia nor orthophosphate is detectable (Table 4.1).

The lowland study area in the Itchen catchment (50°56'N 1°21'W) also has a temperate climate, but with a slightly higher range than at Llyn Brianne (mean stream temperatures 4–18°C) and lower mean annual rainfall (c. 900 mm). The catchment lies mostly on Upper Chalk, and has gravely loams supporting chalk grasslands and heathland. Average hardness exceeds 200 mg/l CaCO₃. Two chalk-fed streams were selected from the 52 previously studied (see Phase I report), to assess biological trends; these were respectively the Cheriton at the source of the Itchen and the Alre. The whole Itchen catchment has been designated as a Site of Special Scientific Interest (SSSI) and Special Area of Conservation (SAC).

Table 4.1 Mean (with standard deviation) values of water quality determinands in the upland and lowland streams selected. For upland LI6, means are based on weekly–monthly data 1981–2005 for pH and 1996–2005 for nitrate. For the lowland streams, mean values reflect monthly data collected from January 1992 to December 2006.

Stream	Determinand	Mean ± standard deviation
Upland LI6	pH Total oxidised nitrogen mg/l Ammonia mg/l Orthophosphate mg/l	6.8 ± 0.2 0.097 ± 0.129 < LoD < LoD
Lowland Cheriton	pH Total oxidised nitrogen mg/l Ammonia mg/l BOD (biochemical oxygen demand) mg/l Orthophosphate mg/l	7.8 ± 0.3 5.89 ± 0.72 0.04 ± 0.02 1.25 ± 0.38 0.035 ± 0.04
Lowland Alre	pH Total oxidised nitrogen mg/l Ammonia mg/l BOD (biochemical oxygen demand) mg/l Orthophosphate mg/l	7.9 ± 0.2 5.05 ± 0.85 0.05 ± 0.06 1.25 ± 0.29 0.075 ± 0.03

Climatic data

Climate data and effects were investigated in the two study areas from 1981 onwards, focusing on the winter conditions prior to spring biological sampling, and on the summer conditions prior to the autumn biological sampling (see below).

For the upland sites, stream temperature trends were determined using a combination of real stream data (monthly means from 16 to 59 months per site), and intercalibrations with (i) continuous data collected throughout the study at the Meteorological Office recording site at Sywdffynon (National Grid Reference SN 693654; 52°16'19"N, 3°54'54"W, altitude 168 m) and (ii) a run of 25 months (1985– 1987) continuously logged (i.e. 15 min) measurements using an automatic weather station operated on Mynydd Trawsnant (SN 825497; 52°7'59"N 3°43'5"W, altitude 340 m) from 1985 to 1987 (see Durance and Ormerod 2007). Linear regressions with high fit were used to calibrate the relationship among stream temperature at Nant Mynydd Trawsnant (LI7), the automatic weather station record on the adjacent Mynydd Trawsnant and air temperature at Sywdffynon (Table 4.2), including adjustments to allow for altitudinal differences using the environmental lapse rate (0.0069°C per metre = 0.173° C).

To represent trends through time in the Itchen sites, values were estimated using temperatures available throughout most of the study period at Eastleigh (38 km from the source at Cheriton, SU 454157, 50°56'20"N 1°21'18"W, altitude 10 m) from daily measurements at 9.00h using a mercury thermometer. Missing values were substituted using a highly significant relationship with air temperature as recorded by the UK Meteorological Office at Eastleigh, 1 km away (SU 449168, 50°56'56"N 1°21'43"W, altitude 11 m; Table 4.2). Work in Phase I showed that this temperature series reflected other chalk-fed sites in southern England nearly perfectly ($r^2 = 0.98$) providing there were small adjustments to account for altitudinal effects and modest groundwater damping in smaller chalk streams. Thus, to reconstruct monthly mean temperatures in

the Cheriton stream and Alre, both within 20 km of Eastleigh (Euclidean distance), values were adjusted (i) to account for altitudinal gains of c. 30 m using the environmental lapse rate and (ii) to account for additional groundwater damping effects using an estimated slope of 0.88 (i.e. b in y = a + bx, where y is the target stream temperature and x is the water temperature in the Itchen at Eastleigh). This value was derived from the average slopes relating stream to air temperature for a range of chalk-stream sites available from Phase I and from the wider literature (see Table 4.2).

To represent long-term hydrological variations at Llyn Brianne, we used discharge data derived from average daily flows at the Plynlimon flume, roughly 37 km to the north at near identical altitudes (SN 853872, altitude 331 m), available from the National River flow Archives (http://www.nwl.ac.uk/ih/nrfa). These data correlate closely with those at other upland gauged sites in the Tywi catchment (Durance and Ormerod 2007). To represent flow trends for the lowland chalk sites, data came from the Itchen at Highbridge (SU 46132112, altitude 16 m), which reflects combined drainage from the Candover Stream, Cheriton Stream and the River Alre. For comparison between upland and lowland sites, and to represent trends through time, discharge values initially in cubic metres per second were standardised within each gauged site by subtraction of the overall mean and division by the standard deviation.

The North Atlantic Oscillation was parameterised using the winter index, covering December, January, February and March, provided by the Climate Analysis Section, NCAR, Boulder, CO, USA; Hurrell 2008). The index is calculated from the difference in sea surface pressure between the Azores and Iceland (Hurrell *et al.* 2003), with positive values associated with mild, wet winters in north-west Europe and negative values with cold, dry winters (Hurrell 1995). This synoptic, climatic indicator is considered to capture many ecological effects, including those affecting streams (Bradley and Ormerod 2001).

Site	b ± SE	
Chalk streams		
Itchen, Eastleigh (SU 454157) ¹	0.76 ± 0.01	
Bere, Dorset (SY 859919) ¹	0.68 ± 0.02	
Avon, Amesbury (SU 151413) ¹	0.51 ± 0.02	
Frome (SY 868861) ²	0.94 ± 0.02	
Lambourne (SU 452693) ²	0.62 ± 0.02	
Winterbourne (SU 453694) ²	0.48 ± 0.02	
Brook (SY 800874) ²	0.74 ± 0.03	
Welsh rivers and streams		
Moorland stream (CI6; SN 772556) ³	0.94 ± 0.04	
Moorland/forest stream (AT; SN 804538) ³	0.97 ± 0.04	
Forest stream (LI1; SN 809529) ³	0.78 ± 0.09	
Plynlimon forest stream (Hafren; SN 8487) ⁴	0.66–0.73	
Plynlimon forest stream (Hore; SN 8388) ⁴	0.51–0.71	
Wye catchment, wooded headwaters ⁵	0.72 ± 0.04	
Wye catchment, main tributaries ⁵	0.94 ± 0.07	

Table 4.2 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 2008; 2: Mackey and Berrie 1991 (for median values); 3: Durance and Ormerod 2007; 4: Crisp 1997; 5: Clews *et al.* in review.

Table 4.3 Regression relationships (y = a + bx) between (i) monthly mean river temperature (y) in the Trawsnant and monthly air temperatures at Sywdffynon (x) over the period 1981–2007; (ii) monthly river temperature (y) in the Itchen and monthly air temperatures at Eastleigh (x) over the period 1981–2007; and (iii) winter stream temperature, winter NAO and sampling year in upland and lowland streams aver the period 1981–2007. See text for grid references of each location (Figure 4.1) and for calculation 'Methods'. *P<0.05, **P<0.01, ***P<0.001.

Location	Dependent variable	Independent variables	a (±SE)	b (±SE)	100.r² (%)	F	n
Upland	Stream temperature, LI6/LI7	Air temperature, Sywdffynon	0.595 (0.390)	0.806 (0.040)	94.7***	394	1, 23
	Winter stream temperature	Year	-66.51 <i>(37.30)</i>	0.036 <i>(0.018)</i>	12.7*	3.65	1, 26
	Winter stream temperature	NAO	4.20 <i>(0.14)</i>	0.247 <i>(0.061)</i>	39.1***	16.07	1, 26
	Residuals winter stream temperature	Year	-100.56 <i>(23.78)</i>	0.050 <i>(0.012)</i>	41.7***	17.89	1, 26
Lowland	River temperature, Itchen	Air temperature, Eastleigh	2.90 (0.18)	0.76 (0.01)	92.0***	2471	1, 242
	Winter stream temperature, Alre/Cheriton	Year	-192.11 <i>(47.03)</i>	0.099 <i>(0.0</i> 23)	41.7**	17.87	1, 26
	Winter river temperature	NAO	_	-	ns	_	_
	Residuals winter river temperature	Year	-217.92 (40.46)	0.109 <i>(0.020)</i>	53.7**	29.0	1, 26

Stream macroinvertebrate data

The upland streams were first sampled for invertebrates in 1981/82 by the Welsh Water (later the National Rivers Authority and Environment Agency; Stoner *et al.* 1984), and from 1985 to 2005 (except 1991) by Cardiff University using identical, quality assured methods (Bradley & Ormerod 2002). To allow direct comparison with the shorter run of data from the lowland chalk sites, trends were investigated here only from 1989 to 2005. Samples were collected in spring (April) annually using standardised kick-samples of 3-minutes total duration aggregated between riffles (2 minutes) and marginal habitats (1 minute) using a hand-net (0.9 mm mesh; 230 x 255 mm; Weatherley and Ormerod 1987, Bradley and Ormerod 2002). Individual animals were identified where practicable to species (i.e. except for Diptera and Oligochaeta), and absolute abundances for each were recorded.

The Cheriton and Alre were sampled for invertebrates between 1989 and 2005 by the Environment Agency using kick-sampling methods across all habitats coupled with a hand search. Note that the upland Welsh streams also involved kick-sampling in all major habitats (margins and riffles), but no hand search. While this difference is

unfortunate, evaluations of sampling efficiency in 1990 and 2001 on the Welsh data illustrate that equivalent sampling effort collected, on average, over 90% of all but the rarest taxa present in each stream, thereby circumventing the need for hand searching (Bradley and Ormerod 2002).

Samples from all the streams studied here were collected at each site in spring around April (March, April and May). In contrast to the Welsh sites, however, invertebrates were recorded at family level and on ordinal abundance scale. From this semiquantitative/family-level dataset, 56 out of an initial 57 families were retained once singletons were eliminated.

In addition to being identified taxonomically, invertebrates for both upland Welsh and lowland chalk sites were classified into six putative functional feeding-groups based on Moog (1995) and adapted to British streams through accumulated field knowledge and literature relevant to UK streams (Hynes 1970). Although subject to some uncertainty, and with some plasticity in feeding methods or omnivory likely in some taxa, the classification has been partly validated using data from stable isotopes (Lancaster *et al.* 2005, S.J. Ormerod and I. Durance unpublished data). In the absence of abundance data for the chalk streams, functional composition was assessed for each sample by counting the taxa (species or families) present in each feeding guild for each sample.

Data analysis

Spring invertebrate assemblages were expected to reflect climatic conditions over the antecedent winter period (December, January, February and March) because of potential discharge and temperature effects during larval development. Autumn invertebrate assemblages were expected to reflect climatic conditions over the antecedent summer (June, July, August and September) because of potential discharge and temperature effects on survival and emergence. Annual winter temperatures were therefore averaged for both lowland and upland streams across the 4 months preceding spring sampling. Annual summer temperature in the chalk sites were averaged across the 4 months preceding autumn sampling (June–September). For discharge, values were averaged for both chalk-fed and upland Welsh streams for 6 months preceding the spring and autumn sampling periods since hydrographs showed distinct partitioning between these half-yearly periods.

Prior to any assessments involving biological data, variations in discharge and temperature were assessed on features expected to be climatically mediated:

- trends in stream temperature between years;
- relationships between stream temperature and the NAO;
- · residuals from the regression of temperature against the NAO;
- discharge trends against year;
- trends in discharge variability using coefficients of variation;
- relationships between temperature and discharge.

With respect to biological data, trends examined included changes through time in:

- abundance (Welsh sites only);
- taxon richness (as family richness in the chalk-stream data);
- taxonomic composition;

• functional composition.

Trends in these variables in relation to antecedent winter or summer (chalk sites only) temperature, discharge and the winter NAO were also assessed. Functional composition was parameterised as guild richness for these analyses, while changes in taxonomic composition were resolved using correspondence analysis (see Durance and Ormerod 2007 for more details).

Methodological assessment

To investigate the effects of data resolution, the Welsh invertebrate data were aggregated to family level (45 families), while absolute abundances were re-cast as a ranked (i.e. ordinal) scale of logarithmic abundance in which 1 = 1-9 individuals; 2 = 10-99; 3 = 100-999; 4 = 1000-9999 etc. This allowed comparisons in the detection of climatically related trends among four datasets respectively with: quantitative, species-level data; quantitative, family-level data; semi-quantitative species-level data; and semi-quantitative family-level data. The trends reported for the Welsh data reflect species-quantitative levels except where stated.

4.3 Results

Climatically mediated variations in upland Welsh and lowland chalk streams, 1981–2007

Mean stream temperatures during winter over the 1981–2007 period in the upland streams ranged from 3.0 to 5.8°C. After accounting for NAO effects, upland stream temperatures increased on average by 1.4°C over this period (Table 4.3, Figure 4.1). In the lowlands, mean stream temperatures in the Alre and Cheriton during winter ranged from 4.2 to 9.2°C over the same years. The lowland streams did not vary significantly with NAO effects, but stream temperatures still increased on average by 2.6°C (Table 4.3, Figure 4.1). Both in upland and lowland streams, summer temperature trends were weaker and neither was formally significant.

Discharge at the upland sites, as represented at the Plynlimon flume, varied in winter from 0.41 to 1.01 m/s (i.e. by 246%) and in summer from 0.14 to 0.54 m/s (385%), but there were no trends through time (Figure 4.2). Relative drought periods over the recording period included winter 1985 – winter 1986; winter – summer 1996, summer 1990 – winter 1992 and winter 2003 – winter 2005. There was some evidence that these effects tracked variations in the NAO variations.

Flows in the lowland Itchen at Highbridge ranged in winter from 3.54 to 12.04 m/s (by 340%) and in summer from 3.11 to 7.22 m/s (by 232%) and, as in the upland sites, there were no significant trends through time. Nevertheless, plots of standardised discharge reveal increasing flow amplitude from year to year both in summer and winter, notably after 1990 (Figure 4.2); high flow periods occurred in winter 1994 – winter 1995 and summer 2000 – summer 2001, while drier years were winter 1991 – winter 1992, winter 1996 – winter 1998 and winter – summer 2005. As a consequence, coefficients of variation have increased in lowland chalk streams in recent years, a characteristic not apparent in the upland Welsh sites (Figure 4.3).

A further recent characteristic of lowland stream discharge has been a relationship with winter temperature. Over the 1981–2005 period, winter discharge and winter temperature were not significantly correlated. However, over the 1989–2005 period in the lowland Itchen (i.e. the period covered by invertebrate data), winter temperatures

were greatest in years marked also by higher discharge ($r^2 = 40.4\%$, P<0.01, $F_{(1, 15)} = 10.2$). No similar effects occurred in upland Wales.



Figure 4.1 Temperature trends in upland Welsh streams and lowland chalk streams from 1981 to 2007 before and after accounting for the effects of the NAO. Note the different scale in the two lower panels.



Figure 4.2 Recent variations in winter and summer discharge in upland Welsh and lowland chalk streams (1981–2007).



Figure 4.3 Moving coefficient of variation in standardised discharge (5-year moving SD/average x 100%) in upland Welsh and lowland chalk streams, 1981–2007.



Figure 4.4 Relationship between stream temperature and discharge in winter in upland Welsh and lowland chalk streams, 1981–2007. The trend for the lowland streams is significant ($r^2 = 40.4\%$, P<0.01, $F_{(1, 15)} = 10.2$).

Recent ecological links to climatically mediated trends in upland Welsh and lowland chalk streams, 1989–2007

The above contrasts and similarities in climatic effects between upland and lowland streams provide circumstances in which invertebrate trends might also have shown contrasts and similarities, and this possibility is now evaluated.

Abundance

Confirming trends revealed previously over a greater time span (Durance and Ormerod 2007), abundance declined with increasing winter temperature in the upland streams from 1989 onwards by an average of 34.5% of the mean value (1528 animals per sample) for every 1°C rise, with temperature explaining 28.8% of variance (Table 4.4a). Similar trends could not be evaluated in the lowland streams due to the type of data available (semi-quantitative data as abundance categories).

Richness

In neither upland nor lowland chalk streams were there any relationships between discharge, temperature or richness (Table 4.4a, b).

Taxonomic composition

In the upland Welsh sites, species composition varied with winter temperature as reflected in significant effects on DCA axis 1 (axis length 2.25 SD; Table 4.4a). Species characteristic of cooler years included *Sericostoma personatum, Ancylus fluviatilis* and *Drusus annulatus*, consistent with an earlier analysis over longer timescales (Durance and Ormerod 2007). However, no effects of varying discharge could be detected.

In direct contrast, in the lowland chalk streams taxonomic composition varied with discharge on DCA axis 1 (axis length 0.79 SD) (Table 4.4b)., as elaborated in Chapter 3

Functional guilds

In the upland streams, no linear trends in guild composition could be detected with discharge or temperature over the period considered. In contrast, in lowland chalk streams, the richness of both grazer and filtering families increased following periods of increased discharge (Table 4.4b).

Methodological investigation

In the upland streams, several results were markedly affected by the level of taxonomic resolution and/or quantification in the data (Table 4.4a). The measurement of total abundance was unaffected by taxonomic resolution, so relationships here were unaffected. Similarly, trends in taxonomic composition with temperature were unaffected by level of quantification, implying most effects reflected changes in species composition over species-specific abundance. By contrast, however, no effects of temperature on upland assemblages could be detected when data were treated at family level implying that species-level changes within families were an important source of trend.
Table 4.4a Significant regression relationships (y = a + bx) between invertebrate assemblages and climatic variables in the upland Welsh streams between 1989 and 2005 (* P<0.05, ** P<0.01, *** P<0.001). The effects of different levels of invertebrate data resolution are shown.

Location	Dependent variable	Quantification	Taxonomic level	Independent variables	a (±SE)	b (±SE)	100.r²	F	n
Wales (LI6)	Total abundance	Quantitative	Either	Log (winter temperature °C)	5515 (1585)	-2541 (1006)	32.9*	6.38	1, 14
	Richness	Either	Either	No significant effect					
		Quantitative			-1.130 (0.536)	0.237 (0.109)	26.5*	4.69	1, 14
	Taxonomic composition CA1	Semi- Quantitative	Species	Winter temperature °C	-1.124 (0.546)	0.2349 (0.111)	25.4*	4.43	1, 14
		Quantitative Semi- Quantitative	Family	No significant effect					
	Functional composition	Either	Either	No significant effect					

Table 4.4b Significant regression relationships (y = a + bx) between invertebrate assemblages and climatic variables in the lowland chalk streams between 1989 and 2005. (* P<0.05, ** P<0.01, *** P<0.001).

Location	Dependent variable	Quantification	Taxonomic level	Independent variables	a (±SE)	b (±SE)	100.r ²	F	n
	Abundance	No test possible							
Chalk streams (Cheriton and Alre)	Richness	Semi- quantitative	Family	No significant effect					
	Taxonomic composition CA1	Semi- quantitative	Family	Winter discharge	0.726 (0.152)	-0.070 (0.023)	46.0*	9.60	1, 12
	Functional composition: Grazer richness	Semi- quantitative	Family	Summer discharge	1.698 (1.562)	0.745 (0.315)	27.6*	5.56	1, 12
	Filterer richness		Family	Winter discharge	1.440 (0.572)	0.219 (0.084)	38.0*	6.73	1, 12

4.4 Discussion

The above combination of changing climatic conditions illustrates some similarities, but also some contrasts, between upland Welsh streams and the lowland Itchen. This is true not only in invertebrate trends, but also in the likely environmental responses to climate-change effects. For example, in both regions recent temperature gain has been winter biased as shown in Phase I, but almost twice as rapid in chalk streams by comparison with upland Wales. This is despite the apparent effects of groundwater damping on most chalk streams (Table 4.2). However, such damping effects would be likely to be more important in summer because this effect increases in proportion to air temperature and insolation (i.e. through shading), and also because groundwater contributions to chalk runoff are greatest at this time. Interestingly, the damping effects of riparian woodland or forestry on upland stream temperatures are also substantial, and in some cases at least as large as groundwater effects on chalk streams. This effect is increasingly recognised, and offers potentially important adaptation mechanisms to reducing high-temperature effects on stream systems (Weatherley and Ormerod 1990, Webb and Crisp 2006).

In neither region has discharge volume changed linearly through time, while in both interannual variations have been extremely large (230–385%) relative to the projected effects of future climate change (< 20% of current means). There have, nevertheless, been large fluctuations between drought and high-flow conditions, with significant changes in variability apparent in the lowland Itchen system. Interestingly, increased winter temperatures here have been accompanied by greater discharge volumes, and this is potentially important ecologically in offsetting any adverse effects on chalk-stream organisms of recent temperature gain. Not only might increased velocities support the respiration of cool-water organisms (see Hynes 1970), but also because any increase in water depth might reduce direct heating of the substratum, hence availability of cooler-water refuges for organisms might increase in deeper water (Clark *et al.* 1999). As noted in Section 3.4, discharge also interacts with vegetation cover, which not only provides macroinvertebrate habitat, but also interacts with heat transfer processes by shading the substratum (Webb and Zhang 1999).

There are clear contrasts in invertebrate responses to climate variation between upland Welsh streams and lowland chalk streams. In the former, changes in abundance and composition have tracked temperature despite variations and warming through time being smaller than in chalk streams. These effects were observed previously over longer data-runs (Durance and Ormerod 2007), and there is some evidence from the post-1989 data analysed here that they have intensified. By contrast, in lowland chalk streams free of water quality trends, both invertebrate taxonomic and functional composition have been strongly related to discharge (see Section 3.4). A tentative conclusion would be that cooler, upland streams contain organisms more likely to be sensitive to changes in thermal regime, while chalkstream ecosystems are more affected by varying flow. There are, however, alternative explanations for the observed pattern. First, winter high temperatures in the lowland chalk sites have been strongly correlated with increased discharges, which might have offset adverse warming effects on organisms as indicated above. Second, the quality of data available from chalk streams (family-level with semi-quantitative abundances) might have masked important temperature effects. A direct test of this hypothesis here by re-treating the long-term upland data showed that temperature effects on assemblages would not have been detected at levels of resolution that mimicked Environment Agency monitoring methods. The detection of trends was particularly sensitive to family versus species-level taxonomy, implying that key temperature effects were at the species level.

This test reveals a potential constraint on the capacity of routine Environment Agency data to detect climate-change effects both on past data and if future data collection continues only at family level.

Long-term variations among invertebrates have the potential to act as the basis of predictive models of how assemblages might vary under future climate. In Welsh upland streams, for example, spring macroinvertebrate abundance might decline by around one-fifth for every 1°C rise in temperature. Many core species could persist if winter temperature gain reached 3°C from values over the last 25 years, but 4–10 mostly scarce taxa (5–12% of the species pool) would risk local extinction (Durance and Ormerod 2007). For lowland chalk streams in the Itchen system, we carried out similar simulations using downscaled data from UKCIP 09 (July 2009) and the equations presented in Tables 3.3 and 3.4. The UKCIP 09 data suggest a potential increase in winter precipitation in southern England of 10–15% over current values by the 2020s, and 12-17% by the 2050s (values of maximum likelihood, depending on CO₂ emission scenarios). Estimating likely effects on invertebrate assemblages for increases in winter discharge by 10, 20 and 30% suggest that future climatic effects in winter would shift the composition of invertebrate families by only 2-3%. This is in keeping with observed variations over the period 1990-2005, where there was never more than 20% variation in invertebrate family composition in the Cheriton despite inter-annual variations in discharge of >340% over that same period. As we state elsewhere in this report, however, far more substantial ecological effects from climate change will arise because of the way that current patterns of discharge variability will be augmented, but modelling these stochastic effects is not straightforward. Also, as shown above, family-level data of the type most widely available from Environment Agency monitoring are likely to underestimate true taxonomic changes due to climate.

5 Evidence from distributional data

5.1 Introduction

Although the Environment Agency's data on invertebrates have been widely used in regional or site-specific assessment of trends, there are fewer examples nationally of these data being used to assess change in broad-scale distribution. In part, this reflects the computational resources required to process the large number of samples involved. However, distribution patterns could be instructive in indicating where in England and Wales different taxa occur, and hence whether they might be most sensitive to effects on upland or lowland conditions. Changes in prevalence and distribution could also reveal trends and climatic effects – at least if influences arising from water quality could be excluded. As a drawback, however, family-level taxonomy could constrain interpretation.

Here, as a first step, we investigate the mapping of distributional patterns using the BIOSYS database at family level for a selected array of invertebrates expected to have mostly upland/western or lowland/south-eastern distributions. We also assess how distribution and prevalence have changed over the period for which data are available. No systematic statistical analysis of changes have been attempted, although we illustrate some of the methods that could be used on a region-specific basis.

5.2 Methods

To assess broad-scale patterns in the distribution of example taxa that might be sensitive to climate-change effects, data were drawn from c. 200,000 samples contained in the Environment Agency 'BIOSYS' database. Representative invertebrate families expected to have contrasting distributions were chosen from the Odonata (Cordulegastridae), Ephemeroptera (Ephemeridae, Heptageniidae), Plecoptera (Taeniopterygidae, Nemouridae Perlodidae) and Trichoptera (Rhyacophilidae), ensuring that some important anglers' fly-life groups were included (e.g. Ephemeridae, Heptagenidae). For each family, the prevalence (i.e. the proportion of samples containing each taxon) was calculated in each 10 km grid square in England and Wales for separate periods 'early' (1990–1992) and 'late' (2002–2004) in the run covered by the entire dataset. Note that one restriction on the interpretation of these data is that BIOSYS has some data gaps for the North West Region during the early 1990s, and this is apparent in the resulting plots.

To assess how the prevalence of each target family has changed through time, most analysis was based on a subset of sites (n = c. 1000) at which macroinvertebrate data have been matched to adjacent data on hydromorphology (River Habitat Survey) and chemistry, usually from sites within 1 km on the same watercourse. The intention is that these other data sources could be used to interpret any biological changes. The character and distribution of these sites is known, and there are no major departures from the typical distribution of other Environment Agency biological sampling sites (I.P. Vaughan *et al.*, unpublished). Trends in prevalence through time in this Environment Agency-wide sample were estimated and smoothed for each family using generalised additive modelling, with values standardised so that the first year (1990) was equal to one. Bootstrapping was used to assess 95% confidence intervals.

As an additional example, trends in the region-specific prevalence of one important anglers' family (Ephemeridae) were calculated using identical methods on all available Environment Agency data. In this case, no confidence intervals have been calculated.

5.3 Results

Among the small sample of invertebrate families analysed, national trends in prevalence fell into one of four patterns (Figure 5.1):

- near-linear increase through time (Ephemeridae);
- apparent recent increase accompanied by inter-annual variation (Rhyacophildae, Heptagenidae, Taeniopterygidae);
- inter-annual variation without marked increase or decrease (Perlodidae, Nemouridae);
- apparent decrease through time with some inter-annual variation (Cordulegastridae).

Among these patterns, changes in prevalence following the drought years of 1995/96 and 2003 were particularly striking in nearly every case.

In addition to the overall trends, however, there were marked variations in distribution, and also marked regional changes in prevalence among the taxa. Thus, many of the taxa selected were typical of upland, western and faster-flowing conditions (Heptagenidae, Taeniopterygidae, Perlodidae, Nemouridae, Rhyacophildae), with the western distribution most apparent in the Cordulegastridae. Among this group, there are some indications of a thinning-out in records from Wales and western Britain between 1990 and 2004 (Taeniopterygidae, Perlodidae, Nemouridae; Figure 5.2c, d, e) despite overall stability or increase among these same taxa. In the Cordulegastridae, reduced prevalence is particularly marked in the west despite some colonisation of sites in south-eastern locations (Figure 5.2b). By contrast, the Ephemeridae characterised generally more southern and eastern locations, and the national tendency towards increasing prevalence has been matched in most areas with the exception of southern Wales (Figures 5.2g, 5.3).



Figure 5.1 National trends (with 95% confidence intervals) in the relative prevalence of selected invertebrate families according to generalised additive modelling using Environment Agency data.

Figure 5.2 Distribution maps for selected invertebrate families in English and Welsh rivers.

The following maps are based on data extracted from the BIOSYS database. We did not have data for the North West Region in the early 1990s, hence there is a gap in the data that occurs in every case. Prevalence is a summary of the frequency of occurrence in samples within each 10 km OS grid square.



c) Taeniopterygidae





f) Heptageniidae





Figure 5.3 Regional trends in the relative prevalence of the Ephemeridae according to generalised additive modelling as calculated from Environment Agency data. In this case, no confidence intervals have been calculated.

5.4 Discussion

This preliminary, large-scale analysis illustrates several possible uses of Environment Agency monitoring data that have not been exploited previously. Most notably, the data have been shown here to provide a source of distributional information that also permits a countrywide or regional assessment of family-specific changes through time. All of the families selected show distinct patterns of distribution, ranging from the typical upland/western families to more lowland, southern taxa such as Ephemeridae. These patterns are well known, but the analysis and mapping exercise here reveals a previously poorly exploited element of Environment Agency data. They might indicate potential sensitivity to different aspects of environmental change – for example temperature increase in upland or western taxa by comparison with flow perturbation in southern and lowland areas or channel alterations in either upland or lowland (see Section 4).

In addition to geographical pattern, trends through time are apparent in the data, but none is entirely linear. Fluctuations in prevalence (Figure 5.1) correspond very closely with those produced using LIFE scores and discharge data for a more limited array of Environment Monitoring sites by Monk *et al.* (2008; see Figure 5.4) and there are three key implications. First, these fluctuations probably reflect discharge, with clear effects from the 1995/96 and 2003 periods of low flow (see Figure 5.1). Second, flow-related variations are apparent at the level of individual families across England and Wales in almost every case assessed here. Third, apparent response in the prevalence of individual invertebrate families to changing discharge appears to be rapid, supporting previous investigations of low-flow effects.

Despite the inter-annual fluctuations, however, longer-term trends are also apparent even in the small array of families analysed here. Some important fly-life taxa, such as Ephemeridae (with records likely to be largely made up of *Ephemera danica*) appear to be increasing not only in general prevalence but also range across several areas of England. This is in some contrast to some casual observations about their trends, and reveals the value of widespread systematic monitoring. In Wales, however, there has been a marked reduction in prevalence, and this is reflected in the contrasting trends for this family across regions (Figure 5.3). Significant overall decline is apparent in one particular case – the Cordulegastridae – made up largely of records of the upland/western species *Cordulegaster boltoni*. This species, which in its nymph stage is characteristic of the marginal areas of headwaters, has invaded some areas of south-eastern Britain, but its western prevalence has declined.

One further interesting aspect of distribution apparent for several of the western taxa, particularly the three cooler-water plecopteran families Taeniopterygidae, Perlodidae and Nemouridae, is an indication of some localised reduction in prevalence between the early 1990s and more recent records. Although this trend cannot be held unequivocally as evidence of climate-change effects, especially without supporting information at species level, these changes would be consistent with the effects of increasing temperature observed elsewhere (Durance and Ormerod 2007). These and other similar distributional patterns would now benefit from more detailed analysis, but considerable care is required to account for other influences, notably changes in water quality.



Figure 5.4 Standardised mean LIFE scores (\pm 2 SE) for 1990–2000 and discharge for all 291 sites in the LIFE paired dataset (version 1.03), developed by the Environment Agency (from Monk *et al.* 2008).

6 Conclusions and recommendations

From this array of parallel investigations, we suggest that several lines of evidence now point to emerging effects that are consistent with the impacts of climate-change or inter-annual climatic variation on river invertebrates in Britain and elsewhere. Effects in England and Wales include changes in abundance, composition, distribution and functional character, with temperature gain most implicated in upland locations and inter-annual discharge variations implicated in chalk streams. Future climatic effects on average discharge over the medium term (2020s to 2050s) appear to be small relative to the current scale of inter-annual variation, and current projections suggest only small changes among invertebrates as a consequence (< 2–3% of family composition). Much will depend on how climatic effects increase current variability, and this has not yet been modelled for organisms. Additionally, improving trends in water quality have masked or offset climate-change effects in some lowland chalk streams despite substantial temperature gain over recent decades, and this effect may be widespread on other river types where water quality has improved. One further important caveat is that the type of data available from most Environment Agency monitoring - involving family-level identification - may well have masked or underestimated some climate-change effects.

Despite available evidence, there are still major gaps in understanding the ecological mechanisms involved in climate-change effects on river invertebrates, on the consequences for river ecosystem function, on the consequences for invertebrate predators such as salmonids, on interaction with other stressors, on the best adaptive responses, and on factors affecting resistance and resilience to climate-change effects.

We now recommend:

- That further assessment should be made of the results of combined temperature and discharge effects on aquatic invertebrates, and of how climate change will augment existing patterns of inter-annual variability.
- That the Environment Agency increases support for existing or new invertebrate monitoring networks aimed at detecting climate-change effects on rivers that make increased use of species-level assessment. We stress that important effects will go undetected without species-level identification.
- That general research effort be given to better understanding the mechanisms, ecological and functional consequences of climate-change effects on river invertebrates using a range of approaches, for example long-term data analysis, distributional data, experiments and the use of climate analogues in space and time. The consequences of climate-change for ecosystem function will be highlighted by growing interest in ecosystem services, but these effects will not be captured by current Environment Agency monitoring.
- That more effort is expended on understanding interactions between climatechange effects and other stressors important to the regulation and management of the UK river environment (e.g. abstraction, eutrophication, sediment mobilisation, acidification, flood-risk management, habitat quality).
- That the significance of these results is now considered by the Environment Agency and its sister agencies with respect to how they might inform adaptive responses to climate change in the river environment and riparian zone.
- That factors affecting resistance and resilience to climate change be investigated more fully.

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