A climate change report card for water

Working Technical Paper

7. Climate change and the UK's freshwater ecosystems

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Abstract

1. The sensitivity of freshwater ecosystems to climate change is a fast emerging issue in their research and management. We outline some of the empirical evidence for ecological effects, but draw attention also to knowledge gaps and uncertainties that currently limit the ability to implement management or prediction with confidence.
2. Extensive data from river and lakes in Britain and Europe reveal warming trends over the last 20-30+ years by 0.1-1.0 °C per decade, through warming recently slowed in the UK. Improved long-term heat budgets would improve understanding and future prediction.
3. Long-term changes in river discharge are more difficult to discern against background inter-annual variations that can exceed 350%. There is some evidence of increasing seasonality in Europe as well as large-scale changes in continental runoff. Clarification is required to distinguish anthropogenic effects from quasi-natural fluctuations in Atlantic weather systems.
4. UK lakes also show evidence of long-term warming, but climate change effects are complicated locally by lake mixing processes, stratification in deeper lakes, ice-cover, and internal changes in dissolved oxygen concentrations. There are also marked interactions with eutrophication.
5. Ascribing ecological changes in UK freshwaters unequivocally to climate change is challenging because other long-term trends, notably in water quality, have had large ecological effects. Nevertheless, some ecological changes in Britain and Europe are consistent with warming or varying discharge. They include alterations in the phenology, abundance, composition, occurrence, trait structure and body size of freshwater organisms as well as emergent properties such as food webs. Multiple phenomena are involved, and mechanisms vary between regions, running and standing waters, and upland and lowland environments. Climate change effects on groups other than fish, invertebrates and lake plankton are poorly known, while wetlands are under-represented in empirical studies. Effects on ecological processes and ecosystem services are poorly understood in all freshwaters.
6. Ecological changes caused by climate threaten the conservation of important species or habitats. They will also affect water resources through factors such as cyanbacterial blooms, freshwater restoration, and progress towards good ecological status. Unless correctly diagnosed, effects will confound the bioassessment of freshwater quality and risk affecting functions, ecosystem services and other economic assets derived from freshwaters.
7. Key knowledge gaps about climate change effects on freshwater ecosystems include: (i) the exact ecological mechanisms involved; (ii) interactions with other stressors and iii) the benefits of different options for adaptive management and climate-change mitigation.

Introduction

Three key issues focus the current debate about the effects on climate change on freshwaters.

First, there is increasing evidence that freshwaters contribute disproportionately to global biodiversity measured by unit area or water volume (Strayer and Dudgeon 2010). This feature stems probably from their physical complexity, the wide range of freshwater types found across the Earth, and their natural isolation in separate basins. As freshwaters are also 'hotspots' for human activity, freshwater organisms are at greater risk of extinction than their marine or terrestrial counterparts (Hambler *et al*. 2010). Impairment of freshwater ecosystems is widespread, and in Europe, major regulatory instruments recognise the conservation value of the best example freshwaters (Birds Directive; Habitats Directive) while also mandating restoration back to Good Ecological Status (Water Framework Directive).

Second, the 'ecosystem services' concept – the idea that ecosystems provide utility and benefits to people – is refocusing attention on freshwaters as assets with large, multiple values and major economic importance. Water infrastructure in the UK is valued at over £250 billion, while treatment costs alone approach £200 million annually. Britain's extensive standing waters and 389,000 km of streams and rivers are considered particularly important: they *provide* water for human use and habitat for economically important species such a Atlantic salmon *Salmo salar* and eels *Anguilla anguilla*; *regulate* flooding, erosion, sediment supplies, water quality and pollutant disposal; *support* adjacent wetland, floodplain, estuarine and riparian ecosystems by supplying water, energy and nutrients; and represent large *cultural* value, for example recreation, tourism and simply as inspirational places (Maltby & Ormerod, 2011). Whilst there is still active debate about the ecosystem services paradigm, and about the role of biodiversity in service provision, this new emphasis is likely to reposition many aspects of the valuation, protection, management and restoration of lakes, rivers and their catchments.

Third, fresh waters are considered to be among the most sensitive of all ecosystems to the effects of climate change both directly, and indirectly through interactions with other stressors (after Durance and Ormerod; 2007; 2009). This has become a major issue in freshwater research and management for which the reasons are increasingly well rehearsed. Firstly, river and lake temperatures track rising air temperature closely, particularly in headwaters, as shown by unequivocal warming in rivers on at least four continents (Dokulil et al. 2006; Kaushal *et al*. 2010). Large biological effects are likely because most freshwater organisms are ectotherms, while metabolic activity, production, decomposition and oxygen concentrations are temperature dependent. In lakes, too, thermal regimes influence ice cover and key physical processes such as mixing. Second, all streams, rivers and lakes are linked inextricably to climatic effects on flow pattern and related processes: discharge variations, flood/drought effects, hydraulics, flow-mediated connectivity, and fluxes of solutes and energy between land and water. Finally, climate is likely to interact with other major influences on freshwater ecosystems such as pollution, abstraction, land use change and the effects of invasive non-native species (Wilby *et al*. 2006). Existing climatic phenomena, such as the North Atlantic Oscillation or El Niño/La Niña, illustrate already how river or lake ecosystems and their organisms are influenced by variations in precipitation or temperature between years (Elliott *et al*. 2000; Bradley and Ormerod 2001; George et al. 2004). Climatic variations between regions also reveal large effects on river or lake character (e.g. Bonada *et al*. 2007).

Although climate changes are unfolding differently under different circumstances, all indications are that the magnitude and rate of future effects will be large and rapid. In the temperate UK, for example, mean annual temperatures by the 2050s are likely to be at least 2-3 °C greater than now, with extreme summer temperatures rising well above 30 °C. Whereas rainfall amounts will not change substantially, greater rainfall seasonality is predicted with potentially larger floods and also longer rain-free periods (see UKCP09; Jenkins *et al.* 2009). If realised, all these changes will have profound consequences for freshwater organisms, processes and ecosystem services. An important current need, therefore, is to develop possible management responses that might reduce the worst effects. However, well-informed management responses will depend on greater knowledge about the effects and processes involved: because freshwater ecosystems also reflect the natural and managed character of their catchments, climate-change effects invariably are context-specific and involve interaction with a range of other factors (e.g. pollution, land use, natural geology). Alongside the appraisal of direct climatic drivers in streams, rivers and lakes, understanding these interactions is a major requirement for assessing the extent to which climate change effects might be confounded, exacerbated or masked by other local or large-scale drivers of trend (Ormerod & Durance 2012).

Here, we review some of the evidence available already on changes in freshwater ecosystems that can be linked to climate as reflected by observed trends in discharge and temperature over recent decades. We also review some of the evidence of biological effects in different regions around the world. Although this review cannot be exhaustive in the space available, we attempt to identify critical knowledge gaps with respect to: (i) the mechanisms involved, (ii) the difficulties of understanding interactions with other stressors; and (iii) the inadequate evidence about the effectiveness or different management options as well as the consequences of actions to mitigate climate-change effects.

Empirical evidence of effects and trends

Confounding trends

It is important to establish at the outset that the identification of climate change effects on freshwaters is not straightforward. Climatic effects are just one expression of global change effects that include also changes in pollution, habitat quality, resource exploitation and the distribution of invasive non-native species. Freshwaters are susceptible to all these changes both directly, and through changes in their catchments. Recent studies in one of Europe's largest rivers – the Rhone – illustrate that these effects arise in multiple, with water quality, abstraction, discharge, temperature and invasive species all interacting over recent decades (Floury et al. 2012). In lakes, too, several case studies illustrate how climate change expressions have run alongside changes in nutrient concentrations or species introductions (Thackeray et al. 2008; George et al. 2012; Winfield et al. 2012), and can interact in complex ways – for example where water temperature influences internal P loading (Spears et al. 2012). There are strong indications that increasing nutrients have affected lakes more strongly than climate over recent decades (Batterbee & Bennion 2012 and papers therein), though climate may be an important secondary driver (McGowan et al. 2012).

In some cases, confounding trends must be understood before climatic effects can be identified (Kattel et al. 2008). In other cases, they can offset or mask climate change effects. In southern English chalk streams, for example, recent gains in invertebrates typical of fast-flowing, well-oxygenated waters occurred in spite of rising temperatures and was best explained by improving water quality and increased discharge (Durance & Ormerod 2009). Very recent evidence using EA and NRW data show that these effects may have been a widespread consequence of improving urban water quality across England and Wales (Vaughan & Ormerod 2012 and unpubl. data).

Thermal regimes: rivers

Trends in freshwater temperature are liable to be among the clearest indicators of climatic change and variation. Throughout the world, several data sets now reveal long-term warming – at least up to c 2005-8 when warming slowed. In Europe, river temperatures increased over at least the last 20-30 years prior to this date by up to 1 °C per decade in upland Wales, Scotland, southern English chalk streams, the upper Rhone, the Loire, the Swiss Alps and Austria (Langan *et al.,* 2001; Daufresne *et al.,* 2004; Hari *et al.,* 2006; Durance and Ormerod 2007; 2009; Webb and Nobilis, 2007; Clews *et al*. 2010; Floury et al 2012 see Figure 1). Local variations are also apparent over similar timescales, and in the UK average temperature gains range from ca 0.2 °C per decade in eastern regions to 0.3-0.4 °C per decade in Wales, the North West and the South West (Wilby *et al*. 2010). River temperatures have also increased by similar magnitudes on other continents, including Asia, Australasia and North America. Most recently, Kaushal *et al*. (2010) examined 41 historical data sets from North American rivers, detecting 21 significant, long-term warming trends of 0.1 to 1.0 °C per decade that correlated with increasing air temperature. Although warming occurred across a wide array of locations, effects were fastest in urban areas. Whilst earlier temperature data are likely to have been made by mercury thermometers, from the 1980s onwards electronic recording has usually been involved, with high precision and regular data capture (typically every 15 minutes).

Despite the apparent consistency, clarity and global coherence of these trends, river thermal regimes and heat budgets are complicated by several processes of which some understanding is important in appraising exactly how climate-change effects on rivers are occurring. Local river heating or cooling depends on the relative balance between heat radiation (in or out), friction against the banks and bed, heat exchange with the surroundings (air, bed, banks etc), condensation (a warming effect) and evaporation (a cooling effect) (Webb *et al*. 2008). Rivers also import heat by advection – i.e. inwards transport – through water arriving from their catchments. These effects vary with season, channel morphology, valley topography, riparian vegetation and substratum conditions; hydrological influences on temperature from groundwater contributions, variations in discharge and river regulation are also important (Caissie, 2006).

The best available studies reveal that short-wave radiation resulting from sunlight is a dominant source of river warming in summer, contributing 80% or more of heat gain in unshaded upland rivers (Webb and Zhang 1997, 2004). In these same streams in winter, however, friction with the bed becomes the largest heat source (> 40-70%). Heat losses occur largely through long-wave (infra-red) radiation (40-65%) and evaporative cooling (10-20%) throughout the year, but heat transfer in winter (20-50%) and conductance into the bed in summer (30%) are also important. Cooling and heating processes vary also among stream types. For example, warming of shaded woodland streams by short-wave radiation in summer is secondary to the effects of scattered long-wave radiation and heat transfer (Webb and Zhang 2004). Lowland chalk streams are warmed dominantly by solar radiation, but cooled dominantly by evaporation and heat transfer, particularly when groundwater contributions are warmer than the atmosphere (Webb and Zhang 1997). In Antarctic glacial melt channels, radiation can be responsible for as much as 99% of heat gain (Cozzett *et al*. 2006), while in other glacial streams frictional heating sometimes exceeds radiative heating even though stream temperature tracked radiative heat inputs most closely (Chikita *et al*. 2010).

The main implications of these processes for understanding the role of climate change in stream warming are: (i) radiation and insolation are likely to be the dominant warming mechanisms in unshaded rivers, at least in summer; (ii) relative warming or cooling by direct heat transfer appears only to be important where temperature differences between air and water are increased; (iii) widely described positive correlations between air and river temperature are most likely to reflect radiative heating in both these media; (iv) protecting rivers from insolation, for example by shading, offers a potential strategy for minimising the greatest warming effects. However, understanding long-term warming trends, especially in winter when radiation inputs are small, will require a more thorough appraisal not only of increased heat gain, but also possible reduced heat-losses. These might include river waters entering or flowing through warmer atmospheres, or less heat lost through long-wave radiation during increased cloud cover at low atmospheric pressure. Radiative Advection – i.e. heat transported by water among oceanic, atmospheric, catchment, ground and surface-water components – might also be important. So far, none of the long-term warming trends described above has been assessed using a heat-budget perspective, and this represents an important gap in understanding with important ramifications for adaptive management (see below).

Discharge effects in rivers

Like temperature, variations in precipitation will be a major source of climate-change effects on freshwater ecosystems. In running waters in particular, factors affecting discharge are fundamental to most, if not all, ecological processes. This stems from the pre-eminence of the shape, magnitude and timing of the flood hydrograph as a selective force on river organisms both directly and through its many influences on hydraulics, connectivity, habitat physiography, floodplain inundation, interactions with the riparian zone, and the transport or dilution of sediments, natural solutes and pollutants. Effects might arise not only through changes in average daily discharge, but also through the frequency and magnitude of extreme high or low-flow events.

In comparison to temperature, however, precipitation and discharge patterns in many locations are affected by proportionately large stochastic variations through time and space that make the detection of additional climate-change effects a substantial challenge. In temperate locations such as the UK, both summer and winter discharge have typically fluctuated by at least 300-350% between the driest and wettest years over the last 3-4 decades (S. J. Ormerod, I. Durance unpubl. data). Clear hydrological trends are therefore difficult to differentiate from background variation (Wilby 2006). Some evidence is now emerging of a spatially coherent tendency towards increasing precipitation and discharge at higher latitudes and in NW Europe, with the reverse in SE Europe; these patterns are linked also with evidence also of greater seasonality, with increasing winter discharge (Stahl et al. 2010). Nevertheless, forecasting climate-change effects on discharge also characterised by considerable uncertainty (Fowler and Wilby 2010). In part, this reflects variations between projections from different global circulation models, down-caling tools or hydrological models (Prudhomme and Davies 2009). Similar problems are likely to arise wherever climate change effects on discharge are small relative to existing variation.

At broader spatial extents, altered spatio-temporal patterns in precipitation, soil moisture, runoff and discharge into the world's northern oceans have been apparent from at least the 1970s (Petserson *et al*. 2002). Here, however, there difficulties arise in identifying the drivers from confounding variations among greenhouse gas forcing and quasi-natural effects caused by the North Atlantic Oscillation.

Given the ecological importance of hydrological effects in rivers, improved prediction of climate change effects on precipitation at all scales is an important priority in modelling consequences for river biodiversity and ecosystem services.

Thermal regimes and associated physical changes: lakes

As with rivers, European lake temperature data reveal warming trends. Dokulil et al. (2006) compiled 20-50 years of annual hypolimnetic temperature data from twelve deep lakes spaced across Europe (2 degrees 95'W to 14 degrees 0'E, 46 degrees 27' to 59 degrees 00'N), detecting marked coherence in changes within geographic regions. While hypolimnetic temperatures varied between years, they increased consistently in all lakes by about 0.1 - 0.2 degrees C per decade; these effects tracked large-scale climatic processes over the Atlantic, and the most consistent predictor of hypolimnetic temperature was the mean NAO index for January-May. In the English District, too, there is evidence of warming in both smaller and larger lakes: the northern basin of Windermere warmed significantly in spring by just over warmed degree centigrade between the 1950s and 2010 – most rapidly in the 1980s (Thackeray et al. 2008). In the smaller Blelham tarn, annual temperatures rose significantly by 1.1 ºC between 1968 and 2008 (Foley et al. 2011), with trends similar in Esthwaite (Feuchtmayr et al. 2012).

Complex processes in lakes mean that warming and other climate-related effects can be expressed in markedly different ways that depend on context and local character (Thompson et al. 2009). In particular, factors such as lake mixing processes, stratification in deeper lakes, ice-cover, internal changes in dissolved oxygen concentrations and even feedback processes caused by the aggregate effects of planktonic lake organisms all determine outcomes. For example, Foley et al. (2012) analysed 41 years of data (1968-2008) from Blelham Tarn to determine the consequences of eutrophication and climate warming on hypolimnetic dissolved oxygen, in turn related to thermal stratification. As a result of a progressively earlier onset of stratification and later overturn as the lake warmed, the duration of stratification increased by 38 days over the 41 years while hypolimnetic anoxia increased significantly over time lake.

Complexities arise also where weather conditions linked to warmer temperatures – for example during positive winter phases of the NAO – give rise to wind-induced changes in factors such as lake temperature, duration of ice cover, or the extent or depth of lake mixing (George 2007, Spears & Jones 2010). Large-scale climate systems associated with the NAO or jet stream position illustrate just how context-specific local outcomes can be (George et al. 2004; Strong & Maberly 2011): in Windermere, for example, the strongest NAO correlations were with air temperature, precipitation, the number of days when ice was recorded, and falling nitrate concentrations as more N was taken up by catchment vegetation at high temperatures. In contrast, at Paajarvi in Finland, the strongest NAO correlations were with air temperature and nitrate – but here concentrations increased because of an earlier 'flush' of melt water from the catchment (George et al. 2004).

Context-dependent effects like these mean that the prediction of climate change effects in lake systems will often require site-specific information.

Invertebrates, fish and other organisms: rivers

As with the assessment of changing discharge, establishing long-term climatic effects on freshwater organisms and ecological processes is characterised by several difficulties. The incremental nature of climate change implies that the detection of significant ecological consequences is likely to require decades of observation; existing examples suggest that these should approach as far as possible the 30-40 year timescales currently being used for climate-change projection. This, in turn, means that few such systematic data are available and were initiated or collected mostly for other purposes. Interpretation is therefore often founded on weak inference (i.e. correlation), characterised by assumptions, affected by confounding effects, and limited in scope for definitive interpretation. Experimental studies to investigate processes are difficult at the scales required to mimic those involved in climate change effects on catchment-river-lake ecosystems – though smaller-scale approaches have been attempted and offer potentially support for understanding larger-scale observation (Hogg and Williams 1996). Cross-sectional analyses of rivers with contrasting thermal regimes, caused for example by geothermal heating, also offer potential (Woodward *et al*. 2010a).

Despite these difficulties, available long-term data are now providing increasingly strong evidence that warming effects on freshwater ecosystems are real and possibly widespread – at least as revealed by commonly studied groups. Patterns reflect combinations of changing abundance, changes in species composition, changes in the occurrence of some scarcer taxa and some evidence of a reduction in body size (Daufresne *et al* 2009).

The Llyn Brianne Stream Observatory, in central Wales, provides one of the world's longest records of climate change effects on stream invertebrates. Begun in 1981 and now in its 34th year, the Observatory collects data from replicate streams draining catchments of 70-250 ha in acid moorland, acid conifer, circumneutral moorland and deciduous woodland. The biological data are supported by extensive chemical monitoring, long-term climatic data within and adjacent to the streams and hydrological data. There are extensive land-use data and a long background of ecological process studies, for example, on energetics, stable isotope composition, habitat succession, predator-prey interactions and various other aspects that have led to the publication of over 100 scientific papers. Data from Llyn Brianne were among the world's first to reveal marked warming in upland streams from the 1980s to the present, illustrating also that these effects were moderated by land use but accompanied by pronounced changes in the abundances of organisms (Durance & Ormerod 2007). For example, spring invertebrate abundances have declined with stream warming by around 20% for every 1 °C rise – implying potentially large effects (Durance and Ormerod 2007; Fig 2). In this case, more than 80% of the core invertebrate community persisted through inter-annual temperature variations of around 3 °C, but species typical of cooler-water conditions, e.g. some cool-water Plecoptera and triclads, have nevertheless been lost. The Llyn Brianne Observatory data have also shown clear interactions between the North Atlantic Oscillation and stream invertebrates (Bradley & Ormerod 2001), drought effects on salmonids (Weatherley et al. 1990) and interactions that show how warm, wet winters exacerbate the effects of acidification (Ormerod & Durance 2009). Changes include local extinctions resulting probably from a combination of species interactions, periodic drought and increased temperature (Durance & Ormerod 2010). Current projects at Llyn Brianne include the assessment of climate on carbon dynamics and export, the analysis of analogues for future climate change, the continued analysis of NAO effects on ecological conditions, and interactions between climate change and ecosystem services under the NERC funded BESS project, DURESS.

Trends identified from Llyn Brianne are consistent with other European locations (Daufresne *et al*. 2004; Durance and Ormerod 2007; 2010; Figure 2), and matched by long-term shifts among macroinvertebrates in European lakes where temperatures have also increased (Burgmer *et al*. 2007). In the upper French Rhone, species changes have been linked not only to higher temperatures, but also to decreased oxygen content and extreme hydro-climatic events, such as the 2003 heatwave (Daufresne *et al*. 2007). Shifts from cooler-water to warmer-water taxa have been detected even at family level in streams on other continents, most recently Australia (Chessman 2010; Figure 2). The extent to which these changes in different regions are driven by similar processes is not yet clear.

Effects of inter-annually varying discharge on stream invertebrates are also emerging, but here interpretation depends on understanding the complexity of prevailing flow effects on organisms and the ways in which flow patterns are changing as climate-change effects occur. For example, variations in precipitation in Mediterranean regions of California have been accompanied by variation among invertebrates of contrasting tolerance to low or high flow, leading in some locations to sustained compositional changes (Beche and Resh 2007). Similarly, in Sonoran desert streams, long-term shifts from perennial to intermittent flow conditions have been accompanied by a changing invertebrate composition. Here, progressive change or recovery in species structure following flood events closely tracks previous flow conditions, with inter-annual variations depending on how organisms resisted channel drying, for example by using hyporheic refugia (Sponseller *et al*. 2010). In complete contrast, in glacial-fed alpine systems, the richness, abundance and community composition of stream invertebrates varies with the relative contributions of meltwater to runoff (Brown *et al*. 2007). Different species persist under different conditions, with high endemicity typical of the species-poor communities in peri-glacial channels (e.g. elevated suspended sediments; but low water temperature and conductivity). Glacial retreat now risks reducing the occurrence of such locations, so the extinction of melt-water specialists is a real possibility.

In the UK, substantial variations in the assemblage composition of river organisms have tracked variations in discharge, but recovery has invariably followed (eg Vaughan & Ormerod 2012). Our own work has revealed further permutations of climatically-induced flow changes, not all adverse. For example, increasing discharge appeared to reduce sensitivity to warming among chalk-stream invertebrates (Durance and Ormerod 2009). In other instances, however, increased discharge in warm, wet periods enhanced the negative effects of episodic acidification (Kowalik *et al*. 2007; Ormerod and Durance 2009). In combination, all of these data illustrate how climate-mediated effects on stream ecosystems are highly context-specific.

For various riverine fish, long-term predictions suggest that cold and cool water species will decline substantially as a result of climate warming, with habitat loss likely to be greater among those more restricted distribution and in regions with the greatest warming (Eaton and Scheller 1996). Increasing problems with non-native establishment are also likely (Britton *et al*. 2010). Available trend data are limited, but sometimes consistent with these predictions in revealing changes in abundance and declining occurrence in cooler-water taxa. For example, in the upper Rhone since the 1970s, southern, thermophilic fish species (e.g. chub *Leuciscus cephalus* and barbell *Barbus barbus*) have progressively replaced northern, cold-water fish species such as dace L. leuciscus **(**Daufresne *et al*. 2004). Over longer timescales, warming appears to have affected the range of highly endangered species such as the Atlantic sturgeon *Acipenser sturio* (Lassalle *et al*. 2010). Adverse phenological effects are also apparent through earlier emergence, for example in the declining European grayling *Thymalus thymalus* (Wedekind and Kung 2010). Elsewhere, prolonged drought effects during long-term studies have reduced native fish abundance while increasing threats from some invasive species (Beche *et al*. 2009). In the case of salmonids – important commercially as well as through their conservation status – northern species, such as Arctic char *Salvelinus alpinus,* are liable to be under particular threat. In riverine species, however, and especially those that are long-distance migrants, climatic effects are liable to be extremely complex because of combined changes during early life stages, during smoltification, on migration and at sea (e.g. Jonsson and Jonsson 2009; Kennedy and Crozier 2010). Emerging evidence also suggests synergistic climatic effects between temperature and discharge; hot, dry conditions apparently matched by reductions in juvenile densities (Clews *et al*. 2010). Northward retraction of breeding ranges may well occur, and there is some evidence of temperature increases already reaching limits for successful breeding in some currently occupied locations (Elliott and Elliott 2010). However, despite thermal tolerances and food requirements being sufficiently well known in some salmonids for predictive models, better field data are required on real trends and fitness in wild populations in relation to temperature and discharge (Weatherley *et al*. 1991; Elliott 2009). This need for further field data extends also into groups and processes. Beyond fish and invertebrates, the literature on climate change effects is still extremely patchy (Barlocher *et al*. 2008).

Invertebrates, fish and other organisms: lakes

While climatic processes sometimes have straightforward effects of lake organisms – for example where summer temperatures in Windermere apparently affect fish recruitment (Paxton et al. 2004) – in other cases more complex processes are involved (see above). Not only do these reflect the physical processes outlined above, but also biological interactions. For example warming and lake stability has apparently affected the timing of zooplankton peaks in Esthwaite water as well as interactions among both edible phytoplankton (e.g. *Asterionella*) and cyanobacteria; here,

stable, warm, anticyclonic conditions in summer favour *Microcystis* and *Aphanizomenon* when *Daphnia* production was suppressed (George 2012). Earlier data here had also shown that the relative numbers of *Daphina* and *Eudiaptomus* shifted as cold, calm winters when small flagellates were relatively abundant gave way mild, windy winters when the phytoplankton community was dominated by colonial diatoms. This shift, in turn, was triggered by the NAO (George & Hewitt 1999). In other words, interacting physical changes in temperature and lake mixing driven by the NAO were linked to interacting changes in phyoplanktonic and zooplanktonic communities.

Despite the complex processes involved, some evidence of climate change effects on lakes in the UK is emerging and includes:

- changes in algal phenology in the English Lake District, mediated both by temperature gain (Meis et al. 2009) and advances in stratification (Thackeray et al. 2008), though effects in some cases may be complicated by changing nutrient concentrations (Feuchtmayr et al. 2012)
- changes in zooplankton phenology locally in Windermere, linked to both increasing temperature and altered algal phenology (Thackeray et al. 2012)
- changes in zooplankton phenology more generally and coherently across different parts of Europe, but complicated again by changing nutrient concentrations (Blenkner et al. 2007)
- variations in zooplankton abundance linked to combinations of nutrient concentrations and factors affecting both algal production and lake stratification (George 2012)
- thermal effects on the recruitment of both perch *Perca fluviatilis* (Paxton et al. 2004) and pike Esox Lucius (Winfield et al. 2008) in the English Lake District
- changes in prey use and fish food-web structure in Windermere linked to declining salmonids and increasing cyprinids (Winfield et al. 2012), with both temperature and nutrients implicated

In all these cases, further information is needed on the wider consequences of these changes, as well as clearer identification of the exact processes involved. In some contrast to rivers, mesocosm experiments are providing additional information, and generally confirming the complex interplay between climate and nutrients in mediating ecological change in standing waters (eg Feuchtmary et al. 2010). Similar tools for running waters would be valuable.

Climate change effects on freshwater ecosystems: the bigger picture

Changes of the type described above are probably a partial record of the trends now underway because of changing climate. Moreover, there are clearly data limitations and uncertainties over predictions. Nevertheless, the trends described above carry a range of important ramifications. First, from a conservation perspective, they indicate risks to species, such as Atlantic salmon, which are not only important economically but also figure in the notification of many European rivers under the Habitats Directive (92/43/EEC). Climate change also affects directly the wider ecosystem character of freshwater types that feature in this European Directive as well as in national policy, such as the UK Biodversity Action Plan (http://www.ukbap.org.uk/). Temperature changes of the magnitude apparent not only in upland headwaters, but also in lowland, groundwater-fed chalk streams, might already be having conservation effects (Durance and Ormerod 2007; 2009; 2010). For example, in English chalk streams, winter temperatures during the last 10 years have begun to border the upper developmental limit for the eggs of both *Salmo trutta* and *S. salar* (Elliott and Elliott 2010).

Second, climate change poses risks to the ecological restoration and management of lakes and rivers, for the aims of the EU Water Framework Directive (2000/60/EC). By changing temperature, changing discharge patterns, and interacting with other pressures on freshwaters, climate change might affect organisms in ways that hinder progress to "good ecological status". Examples would be where increased discharge exacerbated problems from sewage treatment overflows, or where elevated temperatures, drought and reduced nutrient dilution exacerbated euthropication (Wilby *et al*. 2006). In some cases, these effects are likely to have consequences for water resource use – for example through cyanobacterial blooms (Kosten et al. 2012). However, there is also a potential opportunity. Climate change was not a major concern when the Water Framework Directive was being drafted, but it now represents an important policy instrument for reducing adverse effects from other pressures that would otherwise be exacerbated under warmer conditions with more variable flow.

Third, the detection of ecological change and status based on freshwater bioassessment might be confounded by climatic effects, for which exact influences on communities are not yet clear. So far, these issues have been explored more fully in North America than in Europe. For example, Hamilton *et al*. (2010) showed that invertebrate sensitivity to temperature and sensitivity to organic pollution are significantly correlated, and attempts are now underway to partition warming effects and isolate changes from other causes (Stamp *et al*. 2010). The resulting tools are likely to be more effective where the identification of traits, genera or species are precise enough to reflect warming effects, discharge effects or both (Lawrence *et al*. 2010).

Fourth, climate change effects imply potential risks to those ecosystem services for which freshwaters are most important – not least the provision of water supply, the regulation of flooding and support for biodiversity both intrinsically and in adjacent ecosystems. At present, knowledge of interactions among climate change, ecosystem processes in freshwaters and ecosystem service provision is insufficiently well developed to know exactly how any impairments might arise. Equally, better knowledge is required to know how to optimise management actions to ensure that ecosystem services are maintained.

All these issues imply a clear need for considerable deepening of how well climate change effects on freshwaters and their catchments are understood. We identify the following three research priorities.

Knowledge gaps and research priorities

Climatic effects on ecological mechanisms and processes

So far, many indications of climate change effects on freshwater ecosystems are based on speculation, review or prediction, or from assessments of long-term change that correlate with either varying discharge or rising temperature. At the very least, there is need to ensure that other confounding aspects of global change are not responsible for such trends (see Durance and Ormerod 2009). Far more important, there is a clear need to move from describing patterns of change to understanding the mechanisms responsible. This is a crucial step in predicting and managing effects. Changes in fundamental freshwater characteristics such as thermal or discharge regime are likely to cause equally fundamental changes to many ecological processes including community metabolism, primary production, nutrient cycling, decomposition, litter retention, predator-prey interaction, food webs, life-history strategy, phenology, altered behaviour, inter-specific competition, the incidence of parasites or diseases, dispersal or invasion and population genetic composition (Traill *et al*. 2010). So far, however, these explicitly ecological and evolutionary aspects of climate change have been very poorly considered in available research yet could be of pivotal importance. For example, in one of only of handful of worldwide studies illustrating mechanisms through which climate-change causes species extinction (Cahill et al. 2013), Durance and Ormerod (2010) showed how inter-specific competition almost certainly interacted with extreme climatic variation in a local extinction event in Wales. Climate-change effects on inter-specific interactions and food availability for organisms may be more widespread than direct physiological effects through thermal tolerance (Cahill et al. 2013). It is germane, therefore, that Woodward *et al*. (2010b, c) have drawn attention to the effects of climate change on the emergent properties of food web character, trophic dynamics and other network aspects of freshwater systems. At even more basic levels, understanding the eco-physiological effects of changing temperature, discharge and changing oxygen dynamics is still limited by data availability in many organisms (Elliott and Elliott 2010; Stamp *et al*. 2010).

Interacting pressures

A further major dimension of climate change is that effects on freshwaters will arise not only directly, but also indirectly through the many other process linking atmospheric systems, catchments, floodplains and riparian zones to freshwater ecosystems. Potential effects of this nature have been postulated widely, involving the possibilities that climate will have widespread effects on land use, point- and diffuse-source pollution, eutrophication, acidification, invasive species, abstraction and a range of other stressors (see Wilby *et al*. 2006; papers in Ormerod *et al*. 2010). Effects extend also to interactions between anthropogenic climate change and existing, large-scale climatic effects such as the Arctic Oscillation, North Atlantic Oscillation and El Niño that already cause variations in discharge or temperature in river and lake systems large enough to cause biological effects (Puckridge *et al*. 2000; Elliott *et al*. 2000; Bradley and Ormerod 2001). In any of these cases, existing stressors or pressures could exacerbate or compound climate change effects; they could mask or hide climate change effects; or they could act as the indirect pathway through which climate change effects are expressed. Ironically, this latter case includes instances where land use change or technological solutions in response to climate change (e.g. renewable energy generation along rivers) serve to cause problems that are locally at least as large as those caused climate change (Aprahamian *et al*. 2010).

So far, the scientific understanding of interactions between climate change and other pressures is limited. In some cases, climate change effects have been most detectable at sites where other problems, such as water quality, are either absent or well understood (e.g. Daufresne and Boet 2007; Dewson *et al*. 2007; Durance and Ormerod 2007; 2009; Viney *et al.* 2007). In other cases, interactions have been revealed between temperature, discharge, stream nutrient dynamics (Caruso 2001, 2002; Hong *et al*. 2005), habitat availability (Cattaneo *et al*. 2004), and impaired recovery from the effects of acid deposition (Durance and Ormerod 2009).

Adaptive management

This is the third major priority, and in many respects is the most crucial and most surprising gap. Accepting that continued climate change is now inevitable, far better evidence is required from which to support and develop adaptive strategies that will reduce adverse effects are far as possible. Again, available knowledge is scant and still largely speculative (e.g. Ormerod 2009; Palmer *et al*. 2009; Wilby *et al*. 2010). Principal recommendations for adaptation include: (i) improving predictions of ecological effects so that ecological effects can be anticipated and managed, while the most sensitive locations can be protected as far as possible; (ii) reducing the associated stressors with which climate might interact, such as point or diffuse pollution and abstraction; (iii) increasing the lengths of river designated for their nature conservation value, targeted for restoration or included in catchment-sensitive agri-environment aimed at benefits for rivers, riparian zones or river corridors; (iv) buffering rivers against temperature gain through the use of judicious riparian shading; (v) maintaining environmental flows in rivers to the extent that desirable organisms and key biological communities are maintained and functional links with catchments and floodplains are restored; (vi) increasing ecological resilience and resistance to climate change – i.e. enhancing features that allow communities of river organisms rivers to withstand climate trends, or to reorganise and bounce back in ways that sustain natural functions; (vii) improving connectivity among river basins as well as of the processes within them.

All these cases require a better evidence-base, but understanding is still rudimentary. For example, the basic characteristics that increase resistance or resilience at genetic, population, community or ecosystem levels are still poorly understood. This is very unfortunate, because potentially there are large benefits in all these suggested actions that extend beyond adaptive management for climate change. A good example is the use of riparian shade. The principles are straightforward and involve either protecting or planting riparian trees in ways that cool summer thermal regimes (Broadmeadow *et al*. 2011). In addition to this thermal damping effect, other generic benefits include sediment retention and bank stabilisation (Larsen *et al*. 2009); energetic subsidies provided by litter and insects (Fausch *et al*. 2010); increased trophic diversity and increased secondary production in woodland streams (I. Durance and S. J. Ormerod, unpubl); woody debris and enhanced habitat heterogeneity (Piegay and Gurnell 1997), and nutrient retention and denitrification (Ranalli and Macalady 2010). However, in the UK objections to riparian planting are made sometimes by interest groups for landscape, angling, and sometimes even nature conservation. We suggest that improved policy instruments, for example linking catchment and riparian restoration to climate change adaptation, need better development, underpinned by experimental evidence, and with benefits that can be demonstrated operationally.

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Figure 1 Recent temperature trends (1981-2007) in upland Welsh streams (redrawn after Durance and Ormerod 2007) and a lowland English chalk stream (redrawn after Durance and Ormerod 2009) before and after accounting for the effects of the North Atlantic Oscillation (see Ormerod 2009).

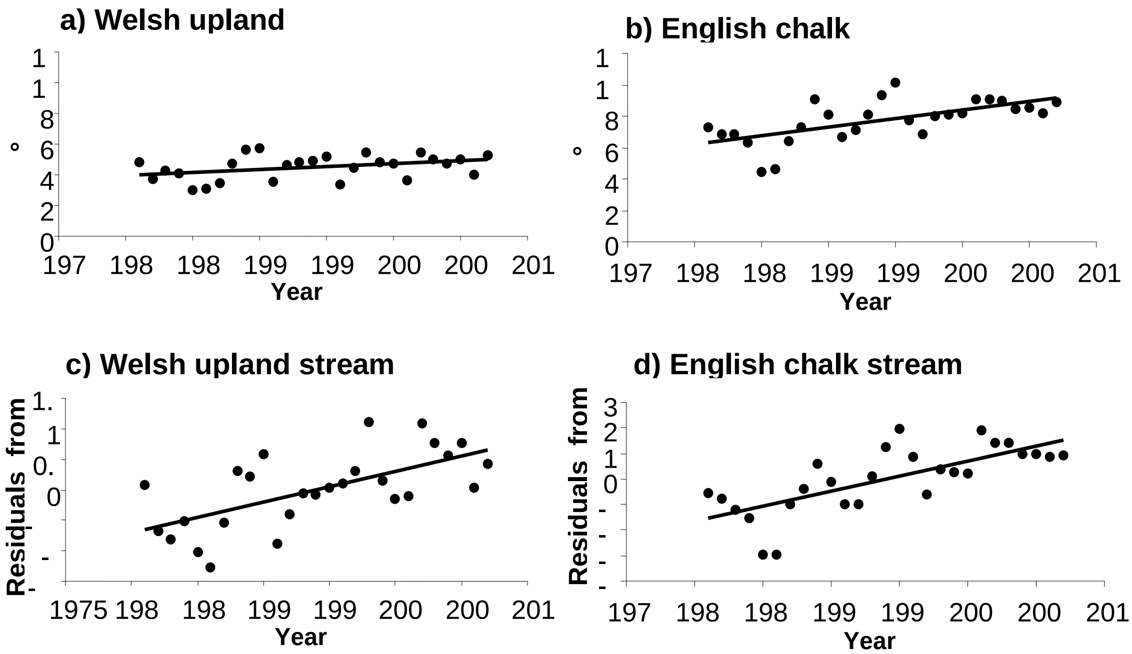

Figure 2. Three examples of biological trends consistent with warming effects in rivers: a) Decline in the catch per unit effort of two cool-water fish species during a period of warming in the Rhone system, France, from 1979-1999 (Daufresen *et al*. 2004); b) Decline in the mean abundance of aquatic invertebrates in two upland streams in the Tywi system, Wales, with increasing winter temperature over a 25 year period (1981-2005) (Durance and Ormerod, 2007); and c) Increases in the odds of capturing warm-water invertebrate families (i.e. those of high thermophily) in streams in New South Wales with sampling date over a 13 year period (1994-2007) (after Chessman 2009)